SPILLOVER AND SPECIES INTERACTIONS ACROSS HABITAT EDGES BETWEEN MANAGED AND NATURAL FORESTS

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Table of Contents

List of Tables

List of Figures

Abstract

We are currently faced with the global challenge of conserving biological diversity while also increasing food production to meet the demands of a growing human population. Land-use change, primarily resulting from conversion to production land, is currently the leading cause of biodiversity loss. This occurs through habitat loss, fragmentation of remaining natural habitats, and resulting edge effects. Land-sparing and land-sharing approaches have been discussed as alternative ways to engineer landscapes to mitigate biodiversity loss while meeting production objectives. However, these represent extremes on a continuum of real-world landscapes, and it will be important to understand the mechanisms by which adjacent land use affects natural remnant ecosystems in order to make local land-management decisions that achieve conservation, as well as production, objectives.

This thesis investigates the impact of juxtaposing production and natural forest on the community-wide interactions between lepidopteran herbivores and their parasitoids, as mediated by parasitoid spillover between habitats. The first and overarching objective was to determine whether herbivore productivity drives asymmetrical spillover of predators and parasitoids, primarily from managed to natural habitats, and whether this spillover alters trophic interactions in the recipient habitat. The study of trophic interactions at a community level requires understanding of both direct and indirect interactions. However, community-level indirect interactions are generally difficult to predict and measure, and these have therefore remained understudied. Apparent competition is an indirect interaction mechanism thought to be very important in structuring host-parasitoid assemblages. However, this is known primarily from studies of single species pairs, and its community-wide impacts are less clear. Therefore, my second objective was to determine whether apparent competition could be predicted for all species pairs within an herbivore assemblage, based on a measure of parasitoid overlap. My third objective was to determine whether certain host or parasitoid species traits can predict the involvement of those species in apparent competition.

My key findings were that there is a net spillover of generalist predators and parasitoids from plantation to native forest, and that for generalists, this depends on

herbivore abundance in the plantation forest. Herbivore populations across the edge were linked by shared parasitoids in apparent competition. Consequently, an experimental reduction of herbivore density in the plantation forest changed parasitism rates in the natural forest, as predicted based on parasitoid overlap. Finally, several host and parasitoid traits were identified that can predict the degree to which host or parasitoid species will be involved in apparent competition, a finding which may have extensive application in biological control, as well as in predicting spillover edge effects.

Overall, this work suggests that asymmetrical spillover between production and natural habitats occurs in relation to productivity differences, with greater movement of predators and parasitoids in the managed-to-natural forest direction. The degree to which this affected species interactions has implications for landscape design to achieve conservation objectives in production landscapes.

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Chapter I
Introduction

1.1 Land-use change as the leading cause of biodiversity loss

Globally, biodiversity is disappearing at an unprecedented rate due to anthropogenic change (M.E.A., 2005). This is cause for alarm because biodiversity is valuable for many direct practical uses (Costanza *et al.*, 1997; Daily *et al.*, 2000), for aesthetic and philosophical reasons (Wilson, 1984; Callicott *et al.*, 1999), and because it maintains the life-support systems necessary for continued human existence on Earth (Chapin *et al.*, 2000; Foley *et al.*, 2005; Hooper *et al.*, 2005). Biodiversity underlies human well-being by providing a great variety of essential ecosystem services (Costanza *et al.*, 1997; M.E.A., 2005). Projections based on different socioeconomic scenarios suggest that biodiversity loss is likely to continue throughout the next century (Pereira *et al.*, 2010). However, these projections show a great deal of uncertainty as to the rate of future biodiversity loss, partly because of the potential for sociopolitical changes to reduce the rate of extinctions (Pereira *et al.*, 2010). We therefore face the challenge of understanding specific mechanisms of biodiversity loss, to the extent that we can make science-based policy decisions with the hope of mitigating further loss as far as possible.

The several most important processes causing biodiversity loss include land-use change (Tilman *et al.*, 2001), climate change (IPCC, 2007), pollution, such as changes to the global nitrogen cycle (Vitousek *et al.*, 1997; Erisman *et al.*, 2013), overexploitation of resources (Rosenberg, 2003), and species invasions (Walther *et al.*, 2009). Of these, land-use change, which results in the loss of natural habitats, has been identified as the leading cause of biodiversity loss in terrestrial systems (Sala *et al.*, 2000). However, opposing the necessity to conserve what remaining natural and semi-natural habitat exists, is the necessity to produce enough food to feed the growing human population, which is predicted to plateau at 9 billion in the middle of this century (Lutz and Samir, 2010). It has been predicted that this will require the production of 70-100% more food (Godfray *et al.*, 2010). Given that land available for conversion to agriculture is increasingly limited, we will need to look for methods of ‘sustainable intensification’, in

which more food and materials are produced without further land conversion to agriculture, and resulting in a lower environmental impact (Godfray *et al.*, 2010).

1.2 Biodiversity conservation versus agricultural production

Critical to balancing objectives of food production against biodiversity conservation will be considering both objectives in land management. Debate has raged between the merits of two contrasting approaches, at either end of a spectrum: land sharing versus land sparing (Green *et al.*, 2005; Phalan *et al.*, 2011; Tscharntke *et al.*, 2012a; Maskell *et al.*, 2013; Fig. 1.1). In the land-sharing approach, also known as wildlife-friendly farming, conservation and production objectives are pursued in the same landscape. Agricultural inputs are less intensive, but biodiversity loss is not as exaggerated as in conventional large-scale farming (Clough *et al.*, 2011). In the land-sparing approach, conservation and production objectives are pursued in separate landscapes. The rationale is that this allows intensification of agriculture in the production landscape, as well as maintenance in protected natural areas of even those species which cannot persist under very low intensity agricultural regimes (Green *et al.*, 2005).

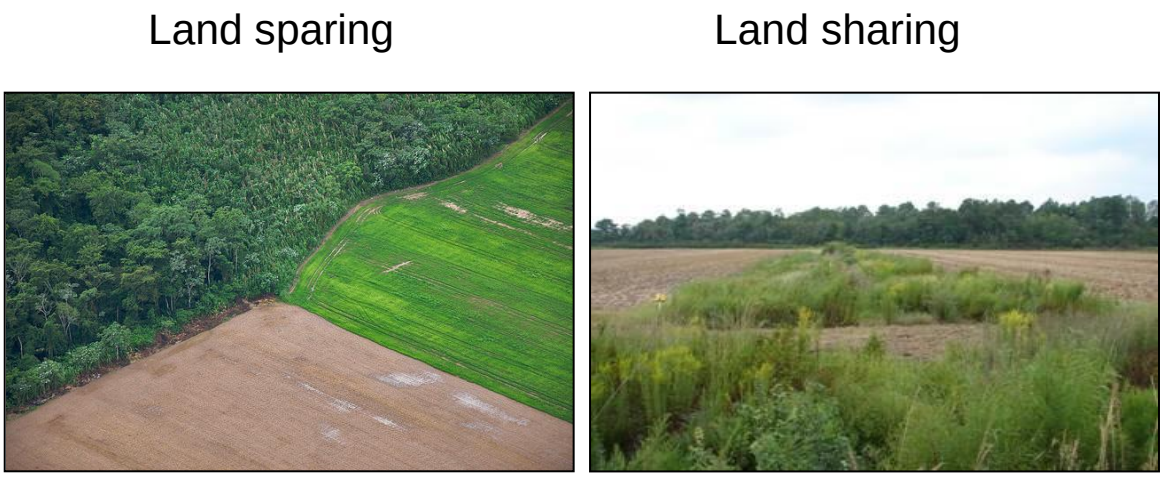

Figure 1.1. Land sparing separates intensive production from natural conservation areas, whereas land sharing integrates agricultural production and biodiversity conservation. (Photos: Sam Beebe, Ecotrust and ncwildlife.org)

A recent study in Ghana and India compared species population densities under varying levels of agricultural yield, compared with baseline densities in forests. The authors found that overall, more species of both trees and birds fared worse than thrived in agricultural settings (Phalan *et al.*, 2011). Thus, assuming that sociopolitical factors do not interfere with proper implementation of land sparing, it seems that this approach may advance biodiversity conservation objectives more effectively than land sharing (Phalan *et al.*, 2011).

On the other hand, Tscharntke *et al.* (2012a) argued that such a dichotomy between approaches is overly simplistic given real world complexity. They cite evidence that land-sharing approaches can produce high agricultural yields, without the costs to biodiversity (Clough *et al.*, 2011) or ecosystem services (Jonsson *et al.*, 2012) associated with the almost complete biodiversity loss in production land under land-sparing approaches. Given that many real-world landscapes fall somewhere in between the opposing land-sharing versus land-sparing ideals, the question of which ideal to aim for becomes less important. Rather, it is necessary to identify specific processes by which landscape management practices affect biodiversity and ecosystem services (Tscharntke *et al.*, 2012b). Equivalently, it is necessary to understand processes by which biodiversity can provide ecosystem services that enhance production objectives (Landis *et al.*, 2000; Bianchi *et al.*, 2006; Garibaldi *et al.*, 2011). Such knowledge could contribute to the goal of engineering landscapes that optimize both conservation and production objectives. This thesis will focus on processes that occur at the edges of natural and managed systems, with the aim of better understanding how conservation and production areas may influence one another in land-sparing-like scenarios.

1.3 Spillover edge effects as a mechanism of change in remnant natural ecosystems

A major process by which habitat fragmentation affects communities in natural remnants is through edge effects (Saunders *et al.*, 1991). Edge effects are changes in a fragmented habitat patch that occur at its edges rather than its interior, and can occur through a variety of biotic and abiotic mechanisms (Murcia, 1995; Ries *et al.*, 2004). Importantly, both the types and magnitudes of edge effects depend heavily on the degree

of contrast of the adjacent landscape with the natural ecosystem (Laurance *et al.*, 2001). In particular, contrasting vegetation structure (Didham and Lawton, 1999) and levels of primary productivity (Polis *et al.*, 1997) between two adjacent habitats may be two of the most important factors determining edge effects. Contrasting vegetation structure across a habitat edge is associated with changes in microclimate at the edge (Didham and Lawton, 1999), which can, in turn, lead to changes in biotic community composition (Campbell *et al.*, 2011).

A difference in primary productivity across an edge can cause 'spillover', or a flow of nutrients and/or organisms between habitats down the productivity gradient (Polis *et al.*, 1997). In terrestrial systems, spillover of organisms, such as predators, between habitats can be an important way in which adjacent ecosystems are dynamically connected (McCann *et al.*, 2005; Tscharntke *et al.*, 2005). Furthermore, the directional nature of this flow, from the higher- to the lower-productivity habitat (Oksanen, 1990; Oksanen *et al.*, 1992), should result in higher-productivity habitats having larger spillover effects on adjacent lower-productivity habitats than vice versa (Polis *et al.*, 1997). Applying this to managed-natural habitat edges, a study of global terrestrial primary productivity found that generally, managed habitats have higher productivity than nearby natural habitats within a region, with only a few exceptions (Field *et al.*, 1998). This led Rand *et al.* (2006) to hypothesize that there may generally be a net spillover of natural enemies (such as predators and parasitoids) from production landscapes into adjacent natural systems (Fig. 1.2), and that this may have far-reaching effects on the biotic communities within the natural ecosystems. Natural enemy spillover from natural to managed habitats has been well-studied, because of its benefits to biological control of insect pests (Landis *et al.*, 2000). However, a recent literature survey found only a handful of published studies that considered spillover of organisms at any trophic level from managed systems into natural systems (Blitzer *et al.*, 2012), and none that considered the community-level impacts of such spillover.

In terms of spillover effects on a recipient habitat, generalist predators, relative to trophic specialists, are predicted to have a particularly significant impact (Rand *et al.*, 2006). This is because trophic generalists should be both subsidized to a higher degree by

high productivity within a habitat, as well as be better able to derive energy from, and thereby suppress populations of, alternate resources in a new habitat (Blitzer *et al.*, 2012).

Natural enemy spillover from managed to natural habitats may therefore be an important process by which juxtaposing intensive production systems and natural conservation areas causes significant change in natural ecosystems. From a landscape-planning perspective, it would be valuable to know the extent to which asymmetrical spillover edge effects occur between managed and natural systems, and what impact this has on both systems.

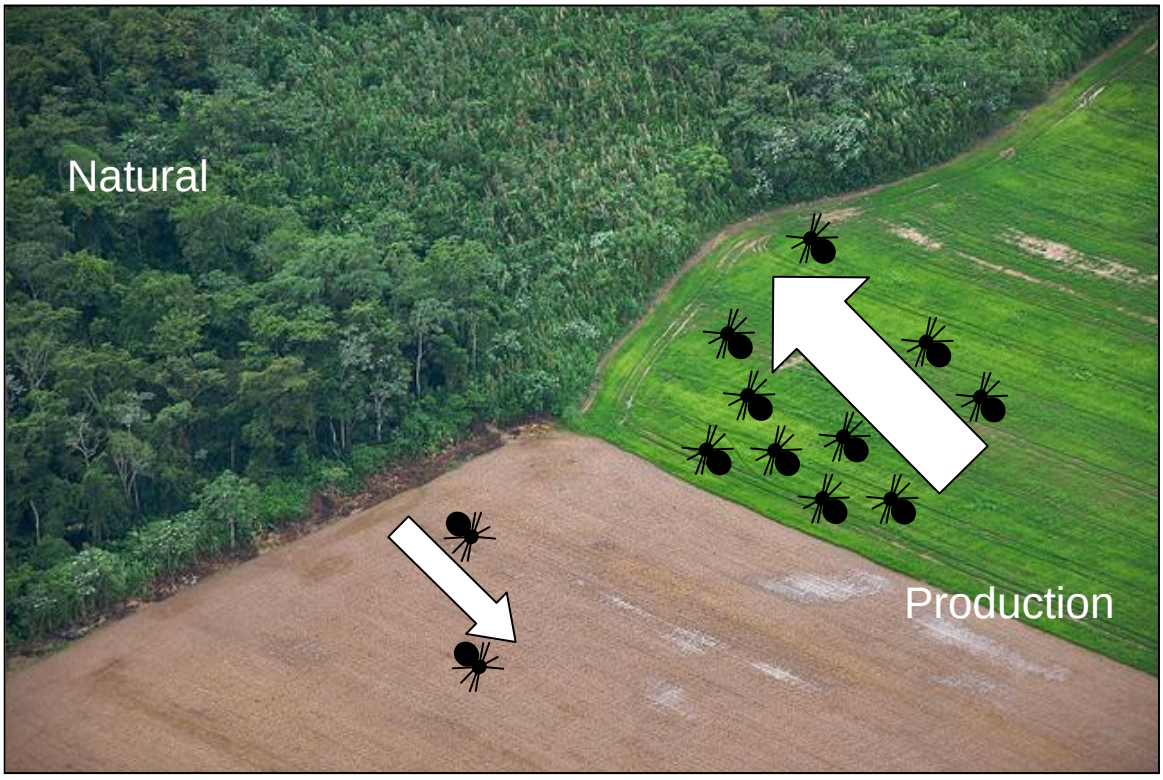

Figure 1.2. There is predicted to be a general net flow of natural enemies from intensive production systems into adjacent natural areas (Rand *et al.*, 2006). (Photo: Sam Beebe, Ecotrust)

1.4 Measuring ecological change: species interactions underlie ecosystem function

Given the complex and dynamic nature of ecological communities, measuring ecologically-significant change following a disturbance, such as spillover of predators

across a habitat edge, is not a straightforward task. Traditionally, biodiversity metrics have been used, most typically species richness, various diversity indices that combine information on species richness and evenness, and changes in species composition (Magurran, 2009). However, more recently there has been a shift towards directly measuring changes in ecosystem function (Didham *et al.*, 1996; Armsworth *et al.*, 2007; Tallis *et al.*, 2008), for example, measuring attack rates by predators, flower visitation by pollinators, or levels of carbon sequestration, since conserving ecosystem function is increasingly recognized to be important (Dobson *et al.*, 2006; Kareiva *et al.*, 2007).

Many ecosystem functions are underpinned by interactions between species (Montoya *et al.*, 2003; Hooper *et al.*, 2005; Thompson *et al.*, 2012). At a community scale, the interactions between species can be depicted as networks, with species as nodes, and links between species representing the energy flow between species during interactions. Food webs are examples of such networks that represent trophic interactions, but any other type of interaction that can be observed in nature (e.g. mutualistic plant-pollinator interactions) can also be analysed as a network (Ings *et al.*, 2009). Interaction networks have allowed comparison of interaction patterns between ecosystems (Memmott, 2009), and the development of hypotheses about which architectural features of networks confer stability on ecological communities (McCann, 2000; Bastolla *et al.*, 2009; Thebault and Fontaine, 2010). Given the clear relationship between interaction structure and ecosystem functioning (Thompson *et al.*, 2012), maintenance of interaction structure is coming more into focus as an important objective of conservation biology (McCann, 2007; Tylianakis *et al.*, 2010).

1.5 Predicting indirect interactions

Interactions in nature can be both direct and indirect. Direct interactions are those typically represented by links in ecological networks, and are obvious and important pathways of energy flow within ecosystems. However, indirect interactions can be as important as direct interactions in determining the abundances and distributions of species (O'Connor *et al.*, 2013). Studies attempting to predict community-wide responses to disturbance have outright failed when indirect interactions were not considered

(Yodzis, 1988), or have found that predictions including indirect interactions were far more accurate than those including only direct interactions (O'Gorman *et al.*, 2010).

Research has highlighted a great variety of mechanisms by which indirect interactions can occur (Wootton, 2002; Orrock and Witter, 2010). Trait-mediated indirect effects (Abrams, 1983; van Veen *et al.*, 2009) can occur when traits of one species change the interaction between individuals of two other species, for example, when herbivory causes a plant to release a volatile that attracts parasitoids (Gols and Harvey, 2009). Refuge-mediated indirect effects (Orrock *et al.*, 2010) can occur between plants when a non-food plant offers a "refuge" to a herbivore, thereby increasing its abundance and predation level on a neighbouring food plant. Strictly trophic, density-mediated indirect interactions can occur in the form of trophic cascades (Carpenter *et al.*, 1985; Knight *et al.*, 2005), also termed 'interaction chains' (Wootton, 1993), and apparent competition or apparent mutualism (Williamson, 1957; Holt, 1977; Morris *et al.*, 2005). Perhaps partially because of the variety of underpinning mechanisms, indirect interactions have thus far been difficult to quantify and predict at a community scale (Montoya *et al.*, 2009), which has limited our ability to predict community-wide responses to disturbance (Yodzis, 1988).

Although typical interaction networks have links representing only direct interactions, they may still be a very useful basis from which to predict a whole class of indirect interactions: those that are density-mediated, such as trophic cascades and apparent competition. This is because the potential effects of a change in density of one node can be traced through its links to more distant nodes, and in this way, potential partners in density-mediated indirect interactions can be identified. Furthermore, the incorporation of interaction strengths into food webs to make them quantitative (Memmott *et al.*, 1994) has made quantitative predictions of density-mediated indirect interactions possible (Müller *et al.*, 1999).

In terrestrial systems, trophic levels often become blurred above the herbivore level, thereby reducing the prevalence of trophic cascades (Polis and Strong, 1996). Consequently, apparent competition may be the most important mechanism by which density-mediated indirect interactions occur (Morris *et al.*, 2005; van Veen *et al.*, 2006). Apparent competition occurs when populations of two species that do not compete for

resources are dynamically linked by shared predators, such that an increase in one species causes a decrease in the population of the other species (Holt, 1977). There are a great many empirical examples of apparent competition (e.g. Schmitt, 1987; Settle and Wilson, 1990; Menge, 1995; Müller and Godfray, 1997; Chaneton and Bonsall, 2000; Östman and Ives, 2003; Oliver *et al.*, 2009; Blitzer and Welter, 2011; Long *et al.*, 2012; van Nouhuys and Kraft, 2012), and a large body of theoretical work suggests that it should have important effects on species abundances and distributions (Holt, 1977, 1984; Holt and Kotler, 1987; Holt and Hochberg, 2001; Abrams, 2004; Brassil and Abrams, 2004).

There are several mechanisms by which predator responses to prey population growth can cause apparent competition. Timescales vary from within one prey generation, through aggregative (Müller and Godfray, 1997) or functional responses (Long *et al.*, 2012), to between prey generations, through numerical responses (Bonsall and Hassell, 1997). Theoretically, apparent mutualism is equally possible, if the shared predator can be satiated or switches to the most abundant prey species in the short term (Holt, 1977), thereby releasing less-abundant prey from consumer pressure. Apparent mutualism could occur over the longer term if the population of one prey species cycles, such that it repeatedly satiates a predator, and thus repeatedly alleviates predation pressure on another prey species that shares the predator (Abrams *et al.*, 1998). However, fewer empirical examples of apparent mutualism have been documented (Tack *et al.*, 2011; Long *et al.*, 2012; Van Maanen *et al.*, 2012), suggesting that it may be less common in nature.

Despite the great number of empirical examples of apparent competition between isolated species pairs, it is still not clear how important it is as a community-wide structuring force. Although apparent competitive motifs are common in food webs (Bascompte and Melian, 2005), it is not known whether apparent competition is important only among some species within a network, or whether all apparent competitive motifs within networks have significant realized apparent competition.

In an important step towards being able to predict the strength of apparent competition at a community level, Müller *et al*. (1999) developed a statistic, d_{ij}, that predicts the potential for apparent competition among host species within quantitative bipartite host-parasitoid food webs. It measures the proportion of parasitoids attacking

host species *i* that have recruited from host species *j*. Two studies have tested this statistic by estimating d_{ij} for all species pairs within host-parasitoid assemblages, then manipulating abundances of a few select host species that were predicted to have a strong apparent competitive affect on other species (Morris *et al.*, 2004; Tack *et al.*, 2011). One found that apparent competition occurred as predicted (Morris *et al.*, 2004), and the other found that indirect interactions sometimes occurred as predicted, but that the effects were positive (apparent mutualism) rather than negative (apparent competition). However, a third, non-experimental study estimated d_{ij}, for all species of hosts within a leaf-miner community, and then followed populations of several species through time. They found no evidence that indirect effects, positive or negative, occurred as predicted according to shared parasitoids, even following a natural population crash of one host species (Kaartinen and Roslin, 2013). It therefore remains unclear whether Müller *et al*.'s (1999) d_{ij} can predict indirect interactions at the scale of an entire host-parasitoid assemblage, and whether indirect effects are generally negative or positive. However, all of these studies tested whether apparent competition affected a focal species as predicted by shared parasitoids with one other species, or at most with several other species, with the effects of each calculated separately (e.g. Tack *et al.*, 2011; Kaartinen and Roslin, 2013). Yet, in nature, a multitude of indirect interactions likely occur simultaneously (Sanders *et al.*, 2013), such that only net effects are visible (Yodzis, 1988). Thus, it is possible that although studies investigating apparent competitive effects for species pairs have found conflicting results, there may be stronger patterns in the magnitude and direction of indirect effects, when the effects are summed over all potentially interacting species within a food web compartment.

1.6 Thesis objectives, study system, and outline

The first and overarching objective of this thesis was to test the hypothesis that a productivity gradient (bottom-up differences in herbivore abundance) drives spillover of predators from managed to natural habitats, and that spillover of predators alters trophic interactions in the recipient habitat. This has only recently been hypothesized as a mechanism by which production land may impact adjacent natural areas (Rand *et al.*, 2006), and should be tested for entire communities. The hypothesis that agriculturally-

subsidized predators may impact adjacent natural habitats is supported by a study of predation on an aphid species by six coccinellid beetle species, which found that predation was higher in crop-bordered grasslands than in grassland-bordered grasslands (Rand and Louda, 2006). However, there has been no study measuring movement of predators across a managed-natural habitat edge that also measures the effects on ecosystem functions such as consumption rates, and no experimental link made between productivity at a lower trophic level and the magnitude of predator spillover.

I carried out this study at a set of forest edges between plantation pine (*Pinus radiata*) and native New Zealand temperate forest (dominated by *Fuscospora* species) in the Nelson / Marlborough region of South Island, New Zealand. Forest edges were 'hard', such that the edge of the plantation forest was very clearly the last row of planted pine trees, which corresponded to an abrupt understorey vegetation change as well. Estimated productivity in plantation *Pinus radiata* forest in New Zealand is 18.4 t CO_2 / ha / yr (Tate *et al.*, 1997). This is roughly twice as high as the productivity of manuka / kanuka scrubland, 7.0-9.0 t CO_2 / ha / yr (Trotter *et al.*, 2005), which is the forest type most similar to that at my field sites (which had a significant manuka / kanuka understorey component), for which productivity estimates were available (http://maxa.maf.govt.nz/forestry/pfsi/carbon-sequestration-rates.htm). This estimated productivity difference is in line with the finding that, in terrestrial systems generally, productivity is higher in managed systems than in natural systems at similar latitude (with the exception of tropical rainforests and savannahs; Field *et al.*, 1998).

Hypotheses about spillover edge effects were conceived with the stark productivity contrast of high-production arable land adjacent to natural areas (e.g. Ovington *et al.*, 1963) in mind (Tscharntke *et al.*, 2005; Rand *et al.*, 2006; Fig. 2.2), and it is unclear whether the smaller productivity and structural contrast between production and natural forest is also sufficient to drive the hypothesized spillover effects. In case it was not, or in case the productivity of natural and plantation forests did not differ considerably in my study region, I used an experimental herbivore population reduction to test the link between habitat herbivore biomass and spillover of predators into adjacent habitats (Fig. 1.3a).

The herbivores that I included in this study were all vegetation-dwelling Lepidoptera species. The generalist predators were common and German wasps (*Vespula vulgaris* and *V. germanica*), and the more specialist predators (parasitoids) included all parasitoid species that were reared from Lepidoptera from these sites (and in Chapter 2, also those parasitoid species that were caught in flight traps and predicted from the literature to parasitize Lepidoptera).

In Chapter 2, I first measured the baseline movement of both trophic generalist predators and more specialist parasitoids across the edge between plantation and natural forest. Next, I experimentally tested the link between herbivore biomass and magnitude of predator spillover from plantation to natural forest, by conducting an experiment in which I artificially reduced the density of all herbivore species in half of the plantation forest edges, and looked for changes in levels of spillover. I tested how spillover of specialist predators (parasitoids) from managed to native forest affects ecosystem functioning in native forest by testing whether parasitism rates in the native habitat changed after experimental herbivore reduction in the adjacent plantation.

In Chapter 3, I tested a specific mechanism by which spillover edge effects are hypothesized to impact recipient habitats: apparent competition (Rand *et al.*, 2006; Fig. 1.3b). I wanted to test whether this mechanism occurred across all species-pairs within a community. Therefore, my second objective was to determine whether apparent competition (or mutualism) could be predicted for all species pairs within a herbivore assemblage based on Müller *et al*.'s (1999) d_{ij}, or the proportion of shared parasitoids. This is not known within any system, let alone across ecosystem boundaries.

Specifically, I wanted to determine whether, following an experimental manipulation of herbivore abundance in one habitat, parasitism rates in the same and adjacent habitat could be predicted based on quantitative information on shared parasitoids, initial attack rates, and the changes in abundance of potential apparent competitors. If parasitism rates were predictable at a community level based on these three pieces of information, this would mean that apparent competition (or mutualism, depending on the sign of the correlation) is a significant structuring force within the herbivore assemblage, across the majority of species pairs. The ability to predict the magnitude and outcome of apparent competition would be a great step forward in terms

of understanding community-wide indirect interactions and ecosystem functioning (Goudard and Loreau, 2008), and has a wide range of potential applications, from predicting community response to disturbance (Montoya *et al.*, 2009), to biological control (Karban *et al.*, 1994; Tylianakis and Binzer, 2013), to predicting impacts of non-native species invasions (Recart *et al.*, 2013) and non-target impacts of biological control agents (Simberloff, 2012).

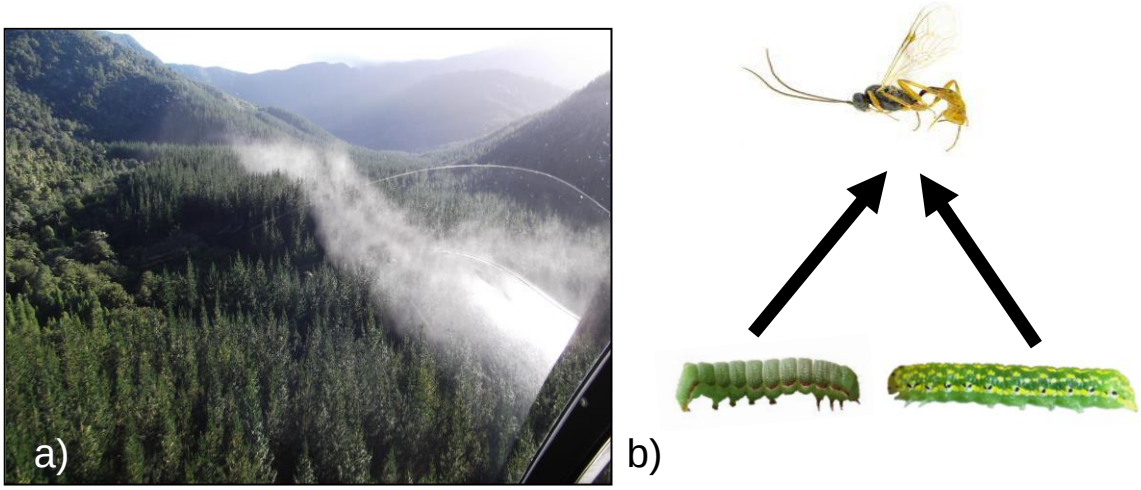

Figure 1.3. a) Experimental herbivore population reduction conducted in plantation *Pinus radiata* forest (right) adjacent to native New Zealand *Fuscospora* species forest (far left). b) Apparent competition (or mutualism) can occur when two herbivore species share a predator. In this study, Lepidoptera larvae were collected and reared to determine parasitism and construct host-parasitoid food webs with which to study apparent competition. (Photos: a) C. Frost, and b) G. Peralta)

After finding that apparent competition does structure entire herbivore assemblages, even across habitat boundaries, and that it can be predicted based on shared parasitoids, my third objective was to determine whether certain host or parasitoid species traits can predict the involvement of those species in apparent competition. If this were the case, it would simplify the prediction of apparent competition. Rather than requiring the amassing of quantitative food-web data, predictions about the degree to which species would be involved in apparent competition might be possible based on non-quantitative food-web data, or perhaps even based on individual species traits, such as body size, trophic generality, or abundance. This predictive ability could be useful in light of my first objective, in that it could be used to predict which species might cause or

suffer from spillover apparent competitive edge effects. It could also be useful in a wide range of other situations where one might want to predict outcomes of apparent competition. In Chapter 4, therefore, I tested whether species traits, either individual or related to their network position, could predict the magnitude of their potential contribution to apparent competition. I used Müller *et al.*'s (1999) d_{ij} as a measure of a herbivore species' potential involvement in apparent competition with each other herbivore species, given that Chapter 3 demonstrated that this measure does indeed predict realized apparent competition at the community level.

Chapters 2-4 are written as manuscripts for submission to international peer-reviewed journals. Finally, Chapter 5 is an overall discussion, in which I synthesize the results from all of the chapters in this thesis and draw overall conclusions, as well as making suggestions for future research.

Chapter II
Community-level spillover of natural enemies

2.1 Abstract

Edge effects in fragmented natural habitats may be exacerbated by intensive land-use in the surrounding landscape. This intensification may be particularly important if cross-habitat subsidies flow from high productivity to lower productivity habitats. Given that most managed systems have higher productivity than adjacent natural systems, subsidised consumers will likely spill over from managed to natural habitats. This may have important effects on ecosystem functioning in the natural habitat. Furthermore, the magnitude and trophic effects of consumer spillover are likely to differ between generalist and specialist consumers, because of differences in resource use. Despite these predictions, it is unknown how commonly managed-to-natural spillover occurs, especially for relatively specialist consumers, such as parasitoids, and what effects this might have on the natural system. I used flight intercept traps to measure spillover of generalist predators (*Vespula* wasps, Vespidae) and more specialist predators (106 species of parasitoids, Ichneumonidae and Braconidae) across habitat edges between native New Zealand forest and exotic plantation forest over an entire summer season. I found net spillover of both generalist predators and parasitoids from plantation to native forest, and that the ratio of individuals moving from plantation to individuals moving from native was greater for generalists than specialists. To test whether natural enemy spillover from managed habitats was related to prey (caterpillar) biomass, I conducted a large-scale herbivore reduction experiment at half of my sites, in which I sprayed 2.5 ha of the plantation side of each edge with a caterpillar-specific insecticide. I monitored bi-directional natural enemy spillover and measured parasitism rates on the native forest side of the edge before and after the herbivore reduction. I found that the herbivore reduction significantly reduced generalist predator but not parasitoid spillover, and that parasitism rates in the native forest were not affected. The effects on natural food webs

of spillover from managed systems, particularly by trophic generalists, deserve more attention in mosaic landscapes containing conservation land.

2.2 Introduction

The effects of loss and fragmentation of natural habitats can be compounded by increases in land-use intensification in surrounding habitats (Saunders *et al.*, 1991; Fischer and Lindenmayer, 2007; Tscharntke *et al.*, 2012b). This occurs through edge effects, caused by high contrast between the natural fragment and the adjacent managed habitat (Murcia, 1995). The level of structural contrast between habitats is an important factor determining edge effects, because it can cause dramatic microclimatic changes at the edge of a natural remnant habitat (Didham and Lawton, 1999; Cadenasso and Pickett, 2000). This can subsequently cause significant shifts in species composition (Campbell *et al.*, 2011).

However, high productivity contrast between habitats may also contribute to edge effects by determining the flow of subsidies into natural fragments (Polis *et al.*, 1997). This can influence ecosystem functioning and stability in the natural habitat (Jefferies, 2000; Huxel *et al.*, 2002). For example, cross-boundary subsidies of nutrients generally increase productivity in recipient systems (Polis *et al.*, 1997; Jefferies, 2000; Sale and Arnould, 2012; Reimchen and Fox, 2013). Likewise, cross-boundary subsidies of organisms, i.e. 'spillover' (Tscharntke *et al.*, 2005; Macfadyen and Muller, 2013), can affect trophic interactions in the recipient habitat (Rand and Louda, 2006; Chalak *et al.*, 2010).

Generally, where a high-productivity habitat lies adjacent to a lower-productivity habitat, subsidies are likely to flow from the high- to the low-productivity habitat (Oksanen, 1990; Oksanen *et al.*, 1992; Polis *et al.*, 1997; Sears *et al.*, 2004). Furthermore, in a study of net primary productivity around the globe, Field *et al.* (1998) found that production land has higher productivity than natural ecosystems in most regions of the world. It is therefore likely that production land generally supports higher densities of consumers than adjacent natural areas, which may lead to a general net spillover of organisms from managed habitats into adjacent natural fragments (Tscharntke *et al.*,

2005; Rand *et al.*, 2006). Although this may cause important changes to ecosystem functioning in natural habitats (Rand and Louda, 2006), these effects have only recently been considered to be a potentially-important mechanism causing fragmentation-related change in natural systems (Tscharntke *et al.*, 2005; Rand *et al.*, 2006). Consequently, they have thus far not been well studied, particularly at the community level (Blitzer *et al.*, 2012).

Most studies of cross-edge spillover to date have focused on movement in the natural-to-managed direction, such as the movement of natural enemies (e.g., Landis *et al.*, 2000; Sackett *et al.*, 2009), pollinators (Garibaldi *et al.*, 2011), plants (Cadenasso and Pickett, 2001), and pest herbivores (Norris and Kogan, 2000) from natural borders into agricultural systems. This spillover has been shown to substantially affect ecosystem services such as natural pest suppression and pollination (Landis *et al.*, 2000; Klein *et al.*, 2007; Garibaldi *et al.*, 2011). Therefore, spillover from managed to natural systems should also be expected to have significant impacts on ecosystem functioning in natural systems (Rand *et al.*, 2006).

Consumer spillover from managed to natural habitats resulting from a productivity difference has been proposed as likely in the case of avian nest predators (e.g. Angelstam, 1986), but this has mostly been speculative (Lahti, 2001; Lahti, 2009; Blitzer *et al.*, 2012). Other than this, the few studies that have examined consumer spillover from managed to natural habitats (herbivores: McKone *et al.*, 2001; Kaiser *et al.*, 2008; Squires *et al.*, 2009; predators: Rand and Louda, 2006; Rand and Tscharntke, 2007; Gladbach *et al.*, 2011), as well as most studies of spillover in the natural-to-managed direction, have been carried out in agricultural landscapes. In these cases, the anthropogenic side of the edge is usually an intensively-managed, fast-growing annual crop. This represents a relatively extreme case of productivity contrast between managed and natural habitats (Ovington *et al.*, 1963), so highly asymmetrical spillover might be expected. Furthermore, temporal resource fluxes related to nutrient inputs and harvesting are also likely to cause pulsed cross-edge spillover in these systems (Ovington *et al.*, 1963; Rand *et al.*, 2006). It is unknown whether cross-edge spillover may be similarly important when there is a smaller cross-edge productivity difference, a relatively small

structural contrast (Eycott *et al.*, 2012), and low-intensity management of the matrix such as between managed plantation forest and natural forest.

Where they occur, spillover edge effects are predicted to be mediated primarily by trophic generalist, rather than specialist, species (Rand *et al.*, 2006). This is for two reasons; first, because generalists are more likely to respond to complementary resources on different sides of the edge (Rand *et al.*, 2006), to couple trophic dynamics in both habitats (Rooney *et al.*, 2006), and therefore to have functional effects in the recipient habitat when spilling over (e.g. Squires *et al.*, 2009). Second, it is likely that generalist predator populations can increase more in response to anthropogenic increases in productivity than can specialists (Symondson *et al.*, 2002). This is because an anthropogenic increase in herbivore productivity would, for a specialist predator, mean an increase in its herbivore prey population, but for a generalist predator, the increase in available resources would be multiplied across all the various herbivore species that it could consume. Therefore, as predator trophic generality increases, so might predator population responses to productivity at a lower trophic level.

Despite this importance of generalists, spillover of relative specialists (parasitoids) from natural to managed habitats (Landis *et al.*, 2000; Macfadyen and Muller, 2013), and in at least one case in the opposite direction (Gladbach *et al.*, 2011), may also occur. Common to all these cases is that the native hosts also occur across the edge in the recipient habitat. However, this suggests that spillover of specialist predators can affect ecosystem processes in the recipient habitat, at least through changes in interaction strengths in existing parasitoid-host interactions in recipient habitats. Yet, because parasitoids may often be extremely specialized (Smith *et al.*, 2006; Smith *et al.*, 2007), even specializing on genotypes within species (Lavandero and Tylianakis, 2013), their trophic impacts on diverse natural habitats may be limited, particularly when plant species composition differs across the habitat edge.

In this study I used a large-scale field experiment to investigate spillover of generalist predators and more specialized parasitoids of lepidopteran herbivores from managed plantation forest into native New Zealand temperate forest. Specifically, I tested the following hypotheses:

1) There is a net spillover of both trophic generalist predators and more specialist parasitoids from managed to natural forest.
2) The ratio of individuals moving in the managed-to-natural versus natural-to-managed direction will be higher for generalist predators than parasitoids, because of generalist predators' greater capacity to respond to habitat productivity.
3) The magnitude of spillover from managed to natural forest is driven by a bottom-up, herbivore-mediated subsidy, such that when herbivore abundance is reduced experimentally, spillover will decrease.
4) Spillover of parasitoids from managed to natural forest affects attack rates in the natural forest, and attack rates will decline if parasitoid spillover decreases.

2.3 Methods

2.3.1 Study System

I selected eight spatial blocks, within which I selected two sites that each comprised an edge between plantation and native forest (16 edges in total). One edge site was randomly allocated as the treatment (herbivore reduction) site, and the other site was designated as the control site within each spatial block. Blocks were at least 2.7 km apart, and sites within blocks were between 1 and 2.7 km apart (i.e. a site was always closest to its paired site). The edges selected were between mature exotic *Pinus radiata* plantation forest and native New Zealand forest in the Nelson/Marlborough region of the South Island of New Zealand (Fig. 2.1).

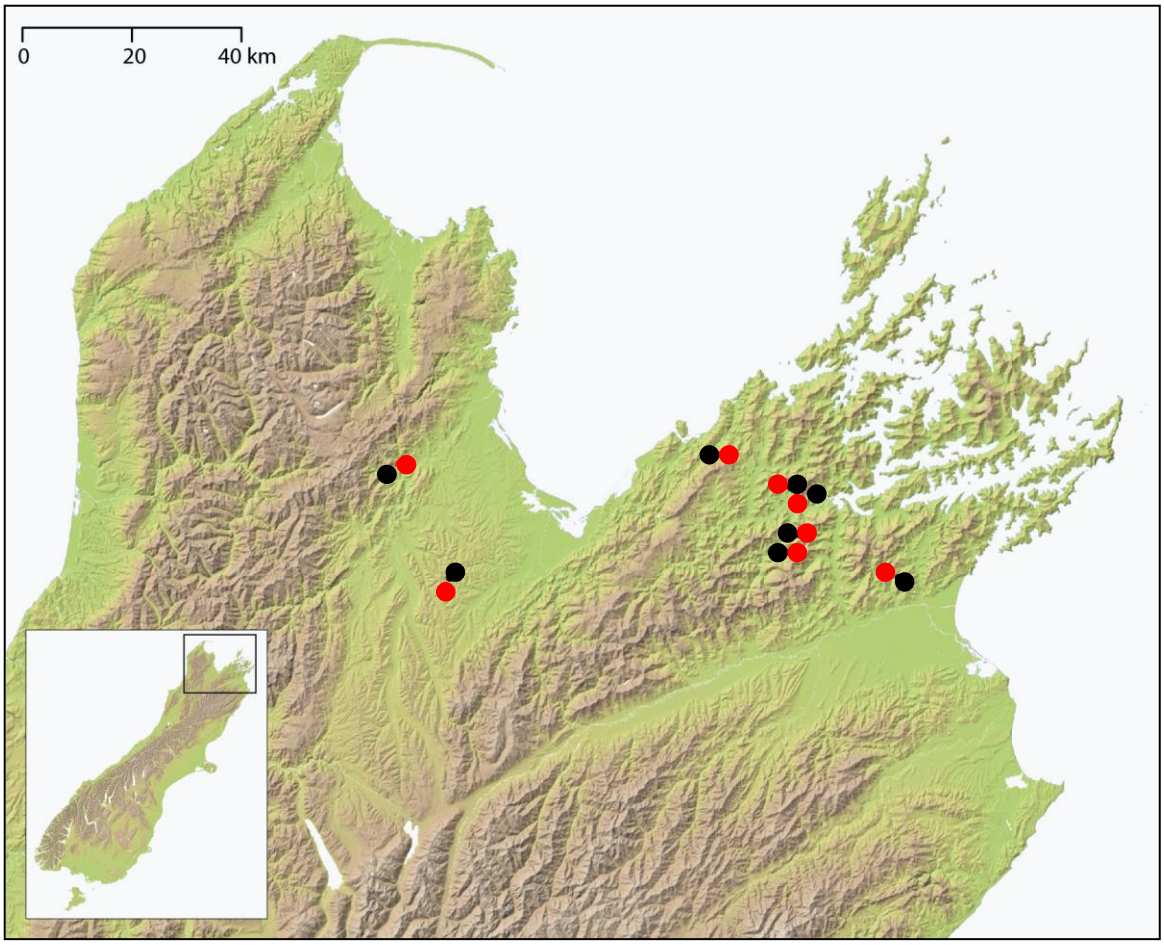

Figure 2.1. Locations of field sites in the Nelson/Marlborough region of South Island, New Zealand. Black points represent control sites, and red points represent herbivore reduction treatment sites.

Plantation forests (usually harvested at 28 years) were at least 17 years old, with mature pine trees and closed canopies, and care was taken to ensure that plantation age was as similar as possible at the two sites within each block. The 'edge' at each site was a hard edge, easily designated as the last row of plantation pine trees abutting the native forest, which corresponded to an abrupt understorey vegetation change as well. Plantation understorey vegetation ranged from dense to almost non-existent and included a range of native ferns, shrubs, and juvenile trees, with the most common species being *Blechnum discolor*, *Pteridium*. *esculentum*, several species of *Coprosma*, *Melicytus ramiflorus*, *Aristotelia serrata*, *Carpodetus serratus*, *Kunzea ericoides*, and *Leptospermum scoparium* var. *scoparium*. Non-natives such as *Ulex europaeus*, *Rubus fruticosus*, and *Leycesteria formosa* were abundant in many sites, and where they were found, they were

often the dominant understorey species. The native forest was dominated by *Fuscospora* species and *Weinmannia racemosa*, with other broadleaf species and the occasional podocarp, such as *Dacrydium cupressinum*, and *Dacrycarpus dacridioides* making up the canopy. There were also patches in which *Cyathea* and *Dicksonia* tree ferns were the dominant canopy species. The understorey vegetation in the native forest included the same native understorey species as in the plantation, as well as many other ferns and broadleaved shrubs (see Appendix 1: Table S1.1 for a complete list of plant species sampled). Occasionally the non-native species indicated above were present, although these were never abundant.

Estimated productivity of planted *Pinus radiata* forest in New Zealand is 18.4 t CO_2 / ha / yr (Tate *et al.*, 1997). This is almost twice as high as the estimated productivity of manuka (*Leptospermum scoparium* var. *scoparium*)/ kanuka (*Kunzea ericoides*)-dominated forest, 7.0-9.2 t CO_2 / ha / yr (Trotter *et al.*, 2005), which made up a large component of the understorey at my native forest sites. This is as compared to, e.g. a five-fold productivity difference between maize and nearby prairie or savanna, and a 25-fold productivity difference between maize and nearby oak forest in Minnesota, U.S.A (Ovington *et al.*, 1963).

2.3.2 Sampling herbivore abundance and parasitism levels

To monitor herbivore abundance and parasitism levels, I sampled lepidopteran larvae both before (October and November 2010) and after (late January and February 2011) herbivore reduction. At each of the 16 edges, I established a pair of 50 m transects parallel to the edge, with one located 10 m from the edge inside the pine plantation, and one 10 m inside the native forest. The 10 m distance was a compromise between a spatial scale over which parasitoids would be able to disperse, and a distance from the edge great enough that the vegetation was distinct from that of the adjacent habitat. I collected lepidopteran larvae from all vegetation within 1 m of either side of each transect, up to a height of 2 m, by beating the vegetation over white sheets until no more larvae fell off. At 5 m intervals along each transect, I also clipped all vegetation up to a height of 9 m within a 1 m^2 area around the transect, using an extendable pole with a clipper head on the end. I beat all clippings over large sheets on the ground to collect the larvae. If

canopy foliage was not accessible over the transect at the designated clipping points, I clipped four or five branches (a roughly standard number of leaves) from the closest tree that had green foliage low enough to reach with my pruning pole. When larva collection along a transect yielded fewer than 50 individuals, I carried out additional sampling outside of the transect until I had collected 50 individuals or had sampled for up to two person-hours. These additional samples were used to supplement numbers of larvae from which to calculate per capita parasitism rates, but were not used in the analyses of larval abundance or number of parasitism events.

I reared the collected lepidopteran larvae to calculate parasitism levels from the parasitoids that emerged. Immediately following collection, larvae were housed individually in small plastic cups, and fed an artificial diet for lepidopterans, specifically designed for beet army worm (Bio-Serv Entomology Custom Research Diets and Environmental Enrichment Products, New Jersey, USA), combined with fresh foliage of the plant species from which each larva was collected. Larvae were reared until they pupated and emerged as adult moths or until adult parasitoids emerged. The parasitoids were identified to species level (using Huddleston, 1986; Austin, 1992; Walker, 1996; Berry, 1997; van Achterberg, 2004), or morphospecies (hereafter "species"). (See Tables S1.2 and S1.3 for lists of Lepidoptera and parasitoid species sampled respectively.)

2.3.3 Measuring spillover of natural enemies across the edge

To compare spillover of natural enemies from plantation-to-native forest versus native-to-plantation forest, I monitored wasp movement across the habitat edge using bi-directional malaise-style flight intercept traps (Appendix 2: Fig. S2.1). I focused on wasps as these made up 92% of the parasitoids reared out of caterpillars. Each trap was hung from a pine tree at the edge, with its 1 m^2 collecting surface parallel to the edge. Two collecting jars on each trap separated the capture of insects flying from the plantation versus the native sides of the edge. I hung four traps along each of the 16 edges: two at 2 m above the ground, and two at 6 - 8 m above ground (depending on the height of possible attachment points). I opened the traps in October 2010, and collected samples in November 2010 and again in early January 2011 prior to my experimental herbivore reduction treatment taking effect. For logistical reasons, the early January 2011

collection actually occurred eight days after the first herbivore reduction treatment, but before the second herbivore reduction treatment. Nevertheless, I considered it to be a "before" collection, since the traps were open for at least 24 days before the first herbivore reduction treatment, and the remaining 8-day period after the first herbivore reduction treatment was not considered long enough for treatment effects to become apparent in changes in wasp movement, as it takes a few days for lepidopteran larvae to die following ingestion of the insecticide. After the two herbivore reduction treatments, I re-sampled all sites in late January, February, March, and April 2011.

I lost small numbers of samples due to storm damage, which led to unequal sampling effort across sites in certain months. To determine whether trap losses occurred in a biased way with respect to my treatments of interest, I used a generalized linear mixed model (GLMM) with a binomial error distribution to model occurrences of missing samples. I included as fixed effects herbivore reduction treatment, forest type, collection date, trap height, and all interactions with herbivore reduction treatment, and included forest type (native or plantation), nested within paired sites, nested within spatial blocks as random factors. Here and in all subsequent analyses, the best model was selected by sequentially removing terms from the initial full model, beginning with interactions, then main effects, and keeping the model with the lower Akaike Information Criterion (AIC) value (Crawley, 2007). I found that in the best fitting model only collection date contributed significantly to the model, and contrasts between levels of collection showed no significant differences (Table S2.1). I am therefore confident that the broken traps should not have significantly biased my treatment effects. Nevertheless, I explicitly include sampling effort as a covariate in subsequent statistical analyses.

From the malaise samples, I removed all of the Hymenoptera. Within these, I conducted further species-level sorting of natural enemy groups comprising generalist predators and more specialist parasitoids. As a measure of generalist predator movement, I sorted and counted two related non-parasitic, invasive species of social wasp *Vespula vulgaris* and *Vespula germanica* (Vespidae). I pooled these non-native species for analysis because they are ecologically similar to the extent that *V. vulgaris*, which arrived later in New Zealand, often now displaces *V. germanica* (Beggs *et al*. 2011). Both species are important predators of Lepidoptera in New Zealand forests (Barr *et al.*, 1996;

Beggs and Rees, 1999). As a measure of parasitoid movement, I sorted and identified the Braconidae and Ichneumonidae. I focused on these two families because most parasitoids that I reared out of the collected lepidopteran larvae were from these families. Because my herbivore-reduction treatment focused on Lepidoptera, I excluded from my analyses any species from genera or sub-families for which no species are known to parasitize Lepidoptera (Gauld, 1984; Wahl, 1993). Some parasitoid species are known to be polyphagous, and thus less specialized than others. For example, the exotic braconid *Meteorus pulchricornis* attacks 21 host species, from nine lepidopteran families in New Zealand (Berry and Walker, 2004). However, as a group, parasitic Hymenoptera are more trophically specialized (Hawkins, 1994) than *Vespula germanica* and *V. vulgaris*, which in the South Island of New Zealand are known to consume species from at least 21 families in nine insect orders and three arachnid orders (Harris, 1991). I deposited all reared and trapped Braconidae in the Museum of Wellington Te Papa Tongarewa (Tables S1.4, S1.5), and all other reared and trapped parasitoid specimens in the New Zealand Arthropod Collection, Landcare Research, Auckland (Tables S1.4, S1.6).

2.3.4 Experimental herbivore population reduction

I sprayed the plantation side of the eight herbivore reduction sites with Delfin WG (Certis, USA L.L.C.), an organic, non-persistent, commercial formulation of *Bacillus thuringiensis* var. *kurstaki*. This bacterial strain kills larval Lepidoptera upon ingestion, but does not affect other insects. I used a helicopter with micron air nozzles (droplet size roughly 100 microns), to spray 2.5 ha of pine plantation at each treatment site: an area 250 m along the edge, centred on the transect for lepidopteran larval collection, and 100 m toward the plantation interior from the edge. I sprayed each of the eight treatment sites twice, on 30 December 2010 and 9 January 2011, both of which were fine days with very little wind, and in most cases I observed no spray drift across the edge into the native forest. In each application, I added 4.5 kg/ha of Delfin WG, mixed with 0.125 L/ha of the wetting agent Du-Wet (Elliot Chemicals Ltd., Auckland, NZ). These amounts and timing were according to the manufacturers' instructions for maximal effectiveness, and comparable to amounts found to be maximally effective against lepidopteran pests (Tortricidae) in North American coniferous forests (Bauce *et al.*, 2004).

My herbivore reduction treatment had the desired effect. I compared lepidopteran larva numbers before herbivore reduction (November collection) and after herbivore reduction (late January collection), on plantation and native sides of the control and herbivore reduction sites, using a (GLMM) with Poisson errors. I included treatment (herbivore reduction versus control), forest type, collection (immediately before versus immediately after herbivore reduction), and their interactions as fixed effects, as well as forest type, within site, within block as random factors. I found that larval numbers did not differ significantly between control and herbivore reduction sites before herbivore reduction, but after herbivore reduction there was a significant reduction in larva numbers in the plantation but not in the adjacent native forest at herbivore reduction sites (interaction effect $Z = -2.76$, $p = 0.006$, Table S2.2). Following the herbivore reduction in plantation forests, I found only 17 % of the caterpillar abundance that we had found in the before-treatment collection, whereas at control sites we found 158 % of the caterpillar abundance from the before-treatment collection.

2.3.5 Statistical Analysis

For all analyses of natural enemy movement, samples from the four traps at each site were pooled into single site-level samples for each forest type, to deal with large numbers of zeroes. For analysis of baseline spillover at control sites (see below), samples were also pooled across collection dates over the entire season. For analysis of the herbivore reduction treatment, samples were pooled across collection dates to create a single 'before' sample and a single 'after' sample at each site for each forest type, since the temporal comparison of interest was before versus after the herbivore reduction treatment.

2.3.5.1 Baseline levels of natural enemy spillover at control sites

To test whether there was asymmetrical spillover of natural enemies across the native-plantation edge (Hypothesis 1), I used data from the control (unsprayed) sites across all collection dates. I used a GLMM with Poisson errors that included the abundance of either trapped generalist predators or the more specialized parasitoids (in separate models) as the response, and the direction of movement (either from plantation

or from native) as a fixed factor. I included site as a random factor to control for the non-independence of edge directions within sites (i.e. each edge had movement from plantation into native and from native into plantation). I also included the number of days during which a trap was exposed, multiplied by the combined intact trap surface area at a forest type within a site (hereafter 'sampling effort'), as a fixed covariate to account for broken traps by removing this source of variation from the error. For Poisson GLMMs where overdispersion was detected, I included an observation-level random effect (Zuur, 2012). All GLMMs were conducted in the lme4 package (Bates, 2011) for R v.2.15.0 (R Core Team, 2012).

2.3.5.2 Movement ratios for generalist predators versus parasitoids

I tested whether the ratio of movement from plantation-to-native forest to movement from native-to-plantation forest differed for generalist predators versus parasitoids (Hypothesis 2). As with Hypothesis 1, I used data from control sites, pooled across collection dates and traps. I calculated the ratio of individuals coming from plantation to individuals coming from native forest for each predator group at each site. This movement ratio was the response variable in a Gaussian GLMM with predator group and sampling effort difference between plantation and native (due to broken traps) included as fixed predictors, and site as a random factor. Assumptions of normality and homoscedasticity were violated, so I log-transformed movement ratio, after which these assumptions were met. I used a Markov Chain Monte Carlo (MCMC) re-sampling procedure to estimate p-values on the final model, as recommended by Bolker *et al.* (2009). The MCMC procedure was carried out using the *pvals.fnc()* function in the languageR package (Baayen, 2010).

2.3.5.3 Natural enemy spillover in response to herbivore population reduction

I expected natural enemies to respond to my herbivore reduction treatment primarily in the first two months following the treatment, because *Vespula* and parasitoid generation times are usually up to c. 30 days (*V. vulgaris* and *V. germanica*: Leathwick, 1997; parasitoids of same genera collected in this study: e.g. Tillman and Powell, 1991; Sarfraz *et al.*, 2008).

For generalist predators, I did not have meaningful before-herbivore-reduction data because *Vespula* wasps only became abundant across sites in the month following herbivore reduction, after the new colonies that were initiated early in the summer had increased in size. Before my herbivore reduction treatment, *Vespula* wasp abundances were very low, and they were not trapped at all in 61% of sites. Therefore, I could not test for a before-after by treatment interaction (as a BACI design), but rather I just compared treatment sites versus control sites after herbivore reduction. For this I used a GLMM with Poisson errors, in which the abundance of generalist predators trapped after herbivore reduction was predicted by herbivore reduction treatment, direction of movement (out of plantation / native) and their interaction. As above, I included sampling effort as a fixed covariate, and site nested within block as random factors.

For parasitoids, I had adequate data both before and after herbivore reduction. Therefore, I used a GLMM with Poisson errors to test whether the abundance of parasitoids trapped was predicted by herbivore reduction treatment, direction of movement (out of plantation vs. native), collection (after vs. before), and their two-way and three-way interactions. I included sampling effort as a fixed covariate, and forest type nested within site nested within block as random factors.

My analyses of parasitoid movement included all trapped Braconidae and Ichneumonidae thought to parasitize Lepidoptera (hereafter "parasitoids"). Since the taxonomy and biology of parasitic Hymenoptera in New Zealand are poorly known, I designated individuals as either Lepidoptera parasitoids or not by using host information from the literature associated with genera or sub-families. To ensure that this decision did not significantly affect the results of my experiment, I re-ran the same analyses on parasitoid movement, but to be conservative I included only the 429 individuals of the species that I had reared out of lepidopteran larvae during my sampling (i.e. confirmed parasitoids of Lepidoptera at my sites).

2.3.5.4 Parasitism levels in native forest after herbivore reduction in plantation

To test the effect of experimental reduction of herbivore abundance in plantation forest on attack rates by parasitoids in the adjacent native forest (Hypothesis 4), I analyzed two measures of the level of parasitism. The first was parasitism rate (the

number of parasitoids reared divided by total number of lepidopteran larvae successfully reared to an adult moth or parasitoid, as a measure of *per capita* impact on hosts), and the number of parasitoids reared (as a measure of *total* consumptive effect of parasitoids). I used GLMMs with binomial errors for parasitism rates and Poisson errors for the number of parasitoids reared, to test whether these were explained by herbivore reduction, collection, and their interaction. I included site nested within block as random factors. In the binomial models I used a cloglog link function, instead of the canonical logit link, because zeroes far outnumbered ones (Zuur, 2009).

In this analysis I considered only parasitism events by parasitoids in the hymenopteran families Ichneumonidae and Braconide, which made up 86% of the reared parasitoids, since these were the families for which I monitored movement. In calculating parasitism rate, I considered all hosts reared successfully to adult moths or parasitoids to have been potential hosts, including those from which non-ichneumonid and non-braconid parasitoids emerged. Because hosts already parasitized by other parasitoids may not have been perceived as potential hosts by Ichneumonidae and Braconidae, I re-ran the parasitism rate analysis with hosts parasitized by other parasitoids removed from the total number of available hosts.

2.4 Results

My trapping effort yielded 1,394 *Vespula* wasps of two species, *V. germanica* and *V. vulgaris*, which comprised my group of generalist predators. I also captured 14,023 parasitic Hymenoptera, of which 1,712 individuals in 106 species were Ichneumonidae and Braconidae in sub-families or genera known to attack larval Lepidoptera. These comprised my group of parasitoids. I collected 4,027 larval Lepidoptera in the native forests, and of these 1,320 were successfully reared through to adulthood or parasitoid emergence, generating 207 parasitoids in the families Braconidae or Ichneumonidae, as well as 30 parasitoids in other taxa not included in my calculations of parasitism levels. Additional sampling away from the transects, in order to increase the accuracy of my parasitism rate calculations, produced another 462 lepidopteran larvae, of which 132

were successfully reared to adult moths or parasitoids. This produced an additional 19 Braconidae and Ichneumonidae and 8 other parasitoid individuals.

2.4.1 Natural enemy levels and ratios of spillover at control sites

Significantly more generalist predators and parasitoids moved out of plantation than out of native forest at control sites (generalists: $Z = 5.77$, $p < 0.0001$: parasitoids: $Z = 4.20$, $p < 0.0001$; Fig. 2.2a, Tables S2.3, S2.4). On average, 88 +/- 48 generalists and 66 +/- 10 parasitoids moved from plantation to native forest, whereas only 22 +/- 13 generalists and 34 +/- 3 parasitoids moved in the opposite direction. The ratio of the number of individuals moving from plantation to the number of individuals moving from native forest was significantly higher for generalist predators than for parasitoids ($t = 3.09$, $p_{MCMC} = 0.0496$; Fig. 2.2b).

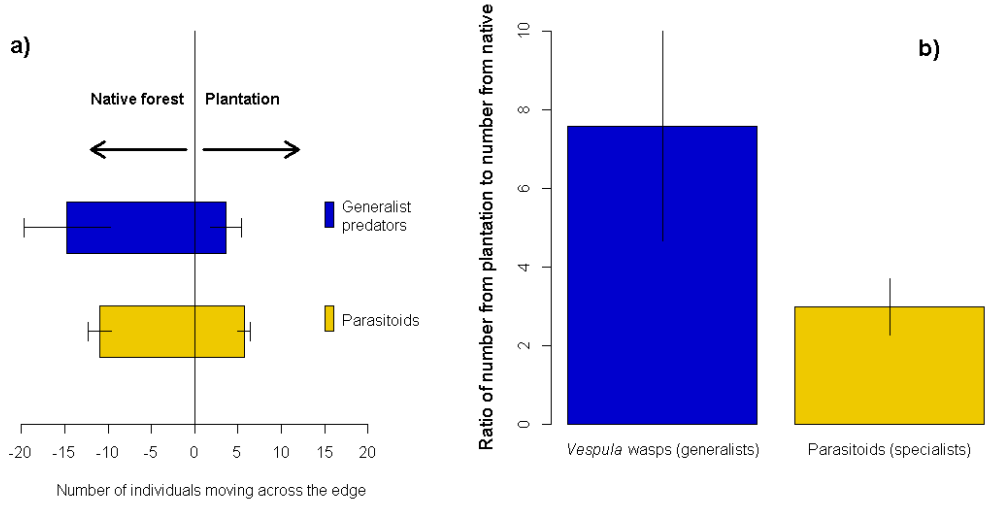

Figure 2.2. a) Movement of predators (generalists) and parasitoids (specialists) out of plantation forest into native forest (direction indicated by negative numbers), and out of native forest into plantation (positive numbers) at control sites, including data from the entire season. The vertical line at 0 represents the habitat edge. b) Ratio of the number of individuals moving from plantation-to-native to number of individuals moving from native-to-plantation forest at control sites for generalist predators and parasitoids. Raw means and standard errors are plotted, although in b) significance was tested using log-transformed data.

2.4.2 Natural enemy spillover in response to herbivore population reduction

In the model for generalist predators, there was a significant two-way interaction between herbivore reduction treatment and forest type ($Z = -5.47$, $p < 0.0001$; Fig. 2.3a, Table S2.5), with significantly fewer generalist predators coming out of plantations subject to the herbivore reduction treatment than out of control plantations, whereas there was no significant difference in the number of generalist predators coming out of native forest in the herbivore reduction vs. control treatments. This suggests that reducing the herbivore population in the plantation reduced the spillover of generalist predators from plantation to native forest. In contrast, the model of parasitoid movement across the edge revealed no significant three-way interaction between herbivore reduction, side of the edge, and collection (the interaction term was removed during model simplification; Fig. 2.3b, Table S2.6). The results from the model of parasitoid movement including only species that were reared from sampled larvae (i.e. confirmed parasitoids of Lepidoptera at my sites) did not differ qualitatively from those obtained using the full dataset (Table S2.7), so I do not consider them further here.

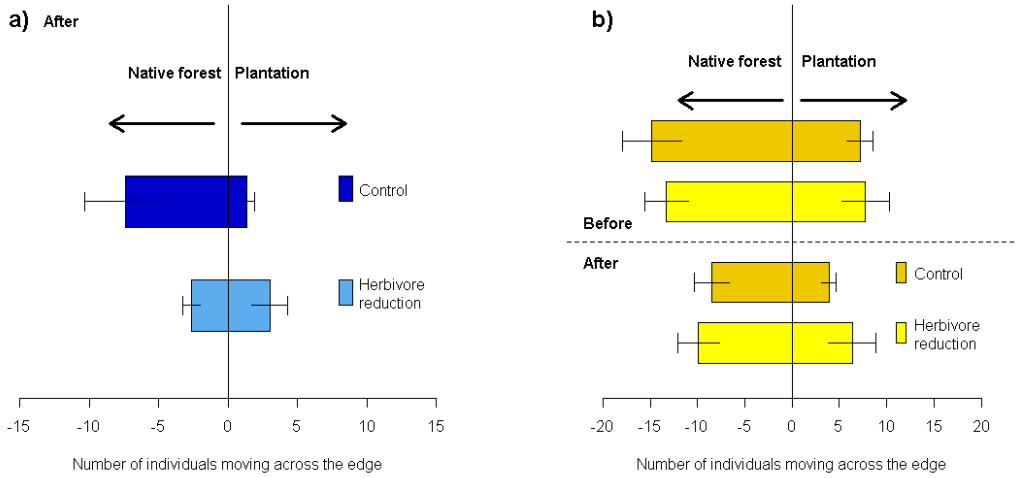

Figure 2.3. Mean (+/-SE) number of a) generalist predators (*Vespula* wasps), and b) parasitoids moving across the habitat edge from plantation to native forest (direction indicated by negative numbers) and from native to plantation forest (positive numbers) before and after experimental herbivore reduction. The vertical line at 0 represents the habitat edge, and bars extending into native or into plantation represent number of individuals moving *into* those habitats from across the edge.

2.4.3 Parasitism in the native forest after herbivore reduction in adjacent plantations

There was no significant interaction between herbivore reduction treatment and collection date for either the model of per capita parasitism rates, or the model explaining the total number of parasitism events in native forest (interaction terms dropped from both models; Tables S2.8, S2.9). This suggests that levels of parasitism in the native forest were not affected by herbivore population reduction in the adjacent plantation. For the model in which hosts parasitized by other parasitoids had been removed from the total number of available hosts in calculating parasitism rates, the resulting significance of the treatment by collection interaction did not differ qualitatively from the first analysis (Table S2.10), so I present only the results from the first analysis.

2.5 Discussion

I found that there was greater spillover of both generalist predators and parasitoids from plantation forest to native forest than in the opposite direction. This finding across an assemblage of parasitoids (relative specialists) is interesting, given that a recent review found that 80% of managed-to-natural spillover was by generalists (Blitzer *et al.*, 2012). This asymmetry supports the hypothesis that there is generally net spillover from managed to natural habitats (Tscharntke *et al.*, 2005). Theory about asymmetrical spillover was developed with highly productive seasonal crops (e.g. Ovington *et al.*, 1963) in mind as the managed habitat (Tscharntke *et al.*, 2005; Rand *et al.*, 2006), and my results demonstrate that asymmetrical spillover can occur even along the shallower productivity gradient found between plantation versus natural forest (Tate *et al.*, 1997; Trotter *et al.*, 2005).

Nevertheless, the ratio of generalist predator spillover out of plantation forest relative to native forest was significantly higher than that of parasitoids. This finding is in line with the hypothesis that generalist predators respond more than specialists to productivity increases (Blitzer *et al.*, 2012), because a productivity increase can multiply available resources to a greater degree for trophic generalists versus specialists

(Symondson *et al.*, 2002). Therefore, the impacts of managed habitats on natural habitats via spillover are likely to be most significantly mediated by generalist consumers (Blitzer *et al.*, 2012).

Furthermore, generalist predator spillover responded to herbivore abundance as predicted, in that spillover decreased significantly following experimental herbivore reduction to 17 % of pre-treatment herbivore abundance. Supporting the assumption that plantation forest had higher herbivore biomass, our flight intercept traps captured significantly more moths moving from plantation to native forest than from native to plantation forest over the entire season (Table S2.11). Altogether, this suggests that the net spillover of generalist predators from plantation to native forest over the season is indeed caused by higher herbivore productivity in the plantation forest (Oksanen 1990).

Unexpectedly, although I observed significant spillover of parasitoids, I did not find a link between herbivore reduction in plantation forest and parasitoid spillover. Congruent with this lack of any changes in parasitoid spillover following herbivore reduction, I found no changes in parasitism in native forests resulting from herbivore reduction in the adjacent plantation. One possible explanation is that invasive *Vespula* wasps might outcompete parasitoids to such a degree that, since *Vespula* invaded New Zealand forests (Beggs *et al.*, 2011), parasitoids may have shifted to fill a slightly different niche, and may recruit mostly from well-hidden lepidopteran hosts (Hawkins, 1994; Hrcek *et al.*, 2013). These hidden hosts in my system could either occur in the leaf litter, or include those that use shelter, such as leaf-rollers (Tortricidae), bag moths (Psychidae), or purse case-makers (Carposinidae). These hidden lepidopteran larvae would perhaps be the least likely to have been affected by my herbivore reduction spray, since they would not have been as likely to feed out on leaf surfaces that were exposed to the spray while it persisted in the environment. Indeed, from my total number of reared parasitoids, 69% were reared from sheltered host species, and it is possible that, had the free-living hosts I collected been left out in the forest and exposed to *Vespula* predation, the percentage of parasitoids reared from free-living hosts would have been even lower by the time the parasitoids were ready to emerge. Thus, it is plausible that limitations of my experiment were responsible for the absence of a link between source habitat herbivore biomass and parasitoid spillover.

Greater subsidy of generalist predators by a productivity difference should therefore cause them to have a greater impact than specialists on prey populations in recipient habitats (Blitzer *et al.*, 2012). This is because generalist predator-prey interaction strengths will be greater after subsidization than will specialist predator-prey interaction strengths. However, generalists should also impact recipient communities more than specialists because they are able to reduce densities of more different resource species than are specialists, and also use resources with greater flexibility. They should therefore be better able to engage in novel predator-prey interactions, such that even a native generalist predator, subsidized in a managed landscape (Rand *et al.*, 2006), might form new feeding links upon spillover back into a source habitat. Generalist predator population dynamics are also less linked to prey population dynamics (Closs *et al.*, 1999), thus making them more likely to drive prey populations to extinction in recipient habitats, particularly when they spill over into a less productive habitat. Spillover of generalist predators may thus be expected to affect the structure and stability of entire food webs through both direct predation and indirect effects, such as competition, apparent competition (Holt, 1977; van Veen *et al.*, 2006), or trophic cascades (Polis *et al.*, 1997).

In the case of the generalist *Vespula* predators considered here, resources (e.g., honeydew in *Fuscospora* forest (Harris, 1991)) on both sides of the edge are likely to be important (Ries *et al.*, 2004; Rand *et al.*, 2006), such that they move back and forth across the edge from the nest location. They could thus be 'ecotone species' (Duelli and Obrist, 2003) that thrive at plantation-native forest edges. In spite of this likely back-and-forth movement, I found a net movement of *Vespula* wasps into native forest. This finding may be due to the way in which experienced *Vespula* foragers navigate during flight; they tend to orient visually, re-locating nests and food sources by recognizing visual cues (*V. vulgaris*: Steinmetz and Schmolz, 2004; *V. germanica*: D'Adamo and Lozada, 2008). It is only the naïve foragers and foragers flying in darkness that use olfactory cues to navigate (Steinmetz and Schmolz, 2004), and so it is likely that my traps caught very few experienced foragers, which would probably fly back and forth across the edge along the same routes, missing my traps on the return flight if they missed them the first time. Therefore, my traps probably caught mostly naïve foragers, and thus should be a good measure of relative abundances of *Vespula* wasps starting from each side of the

edge (and impacting the other side), even if they likely underestimate the total forager movement.

Although, for logistical reasons, I did not measure attack rates of generalist predators as a measure of spillover impact in the native forest, the many ways in which invasive *Vespula* wasps impact native New Zealand *Fuscospora* forest have been well documented (Beggs *et al.*, 2011). In these forests, *Vespula* wasps often reach abundances high enough to affect population growth and persistence of Lepidoptera, and may even cause local extirpation of all free-living lepidopteran larvae except for those emerging in early spring (Beggs and Rees, 1999). *Vespula* wasps in native forests also compete with robins for lepidopteran larvae, stealing food caches made by robins (Barr *et al.*, 1996), and are implicated in the declines of several native bird species in these forests (Elliott *et al.*, 2010). They therefore likely have negative indirect effects on every other predator of lepidopteran larvae as well. Finally, because Lepidopteran larvae are estimated to comprise about 33% of the diet of *Vespula* wasps in this system (Harris, 1991), their abundance in plantation forests likely represents a subsidy to *Vespula* that indirectly impacts other prey taxa in the native forest, although this has not been studied.

In addition to protein resources, *Vespula* wasps forage for carbohydrate resources (Harris, 1991). During periods of highest wasp abundance, they are capable of removing up to 99% of the honeydew produced by *Ultracoelostoma* scale insects in *Fuscospora* forests, which is an important resource for numerous other species, from soil microbes, to insects and birds (Beggs *et al.*, 2011). *Vespula* monopolization of this honeydew resource has been shown to change the soil microbe community from bacterial to fungal dominance, which in turn increases soil carbon and nutrient storage (Wardle *et al.*, 2010). This suggests that, in addition to direct predatory effects, spillover of *Vespula* wasps into native New Zealand forests could have a large impact on ecosystem carbon dynamics (Wardhaugh and Didham, 2006).

This is the first experimental study to test the hypothesized link between productivity (resource abundance) and magnitude of community-wide cross-edge spillover (Blitzer *et al.*, 2012), and has implications for conservation of natural fragments. A recent comparison of land-sparing strategies (keeping conservation land separate from high-production agricultural land), versus land-sharing strategies (integrating

conservation and lower-intensity production land in the same landscape) found that land sparing better maintains biodiversity (Phalan *et al.*, 2011). My results support the minimization of edge-to-interior ratios of conservation areas bordered by production landscapes, but suggest that productivity differences may exacerbate the impacts of managed areas on natural ones (Didham *et al.*, 2012). Given that land-sparing approaches advocate the intensification of production land, my findings provide a caveat to their implementation, because increased intensification will lead to increased spillover into natural habitats. Plantation forest has been advocated as a buffer to protect natural remnants, because it is structurally more similar to natural forest than are agricultural crops (Brockerhoff *et al.*, 2008). However, my study shows that this approach could generate spillover effects on natural forest, perhaps augmented by the structural similarity in habitat types (Eycott *et al.*, 2012). My results suggest that spillover of natural enemies, and the potential ecosystem-level consequences of this type of edge effect, require careful consideration in the management of mosaic landscapes.

Chapter III
Quantitative food webs can predict community-wide attack rates across ecosystem boundaries

3.1 Abstract

All species exist within a complex network of interactions with other organisms, in which indirect effects can propagate widely across species that might never interact directly. Recently, information about shared predators in quantitative food webs has been used to successfully predict indirect interactions among selected pairs of prey species within a given habitat. However, it remains unclear whether these predictions can be scaled up to encompass all the indirect interactions in a food web, and whether the movement of predators between habitats has community-wide indirect effects on herbivores in adjacent habitats. I tested this using parasitoid-host food webs sampled at habitat edges between plantation and natural forests, where spillover of predators may significantly impact ecosystem functioning in the recipient habitat. I constructed an empirical quantitative food web of cross-habitat interactions collected over two years at 'training' sites (68 Lepidoptera hosts and 43 parasitoid species), and used this to predict parasitism rates on hosts at separate 'validation' sites following a large-scale experimental reduction of host abundance on the plantation side of edges. I hypothesized that, if predator-mediated negative indirect interactions are an important mechanism structuring community-wide interaction networks, then parasitism rates of hosts should be predictable given information on the proportions of shared parasitoids between hosts, initial attack rates, and changes in host abundance. I found that observed parasitism rates in the validation sites following experimental prey reduction were significantly correlated with predicted parasitism rates based on the quantitative web training data, whether the predictions were made based on just one or both of the habitats. This provides strong evidence that predator-mediated negative indirect interactions are a community-wide structuring mechanism. These findings could have broad application in biological control,

and in the implementation of land-sparing conservation strategies where cross-ecosystem spillover of predators from production land might threaten adjacent natural ecosystems.

3.2 Introduction

Indirect interactions between species in ecological networks occur when a change in the density or behaviour of one species affects other species beyond those linked in direct trophic interactions. Both theoretical (Holt, 1977, 1984; Holt and Kotler, 1987; Holt and Hochberg, 2001; Abrams, 2004; Brassil and Abrams, 2004) and empirical evidence (Schmitt, 1987; Settle and Wilson, 1990; Menge, 1995; van Nouhuys and Kraft, 2012) suggests that such indirect interactions can significantly alter population growth rates and persistence (Bonsall and Hassell, 1997), and can even be as important as direct trophic effects in altering species abundances and distributions (O'Connor *et al.*, 2013).

Being able to predict indirect effects will therefore be key to a better understanding of ecosystem functioning (Goudard and Loreau, 2008), particularly in diverse communities (Morris et al 2004). It will also help us to better predict outcomes of anthropogenic change (Tylianakis *et al.*, 2008), such as community responses to invasion by non-native species (Mitchell *et al.*, 2006), non-target impacts of introduced biological control agents (Simberloff and Stiling, 1996), and climate-dependent changes to species' traits (Henri and Van Veen, 2011) and interactions (Romo and Tylianakis, 2013). Furthermore, in present-day fragmented landscapes, understanding how habitat boundaries influence indirect interactions will be important in predicting many edge-mediated processes, particularly in land-sparing scenarios (Phalan *et al.*, 2011). These include spillover of biological control agents onto non-target hosts in natural areas (Paynter *et al.*, 2008), effects of natural field borders on crop pest populations (Bianchi *et al.*, 2006), and indirect effects of crop pest outbreaks on neighbouring natural areas (Rand *et al.*, 2006).

Research has highlighted many mechanisms by which indirect interactions can occur (Abrams, 1983; Wootton, 2002; Knight *et al.*, 2005; Gols and Harvey, 2009; van Veen *et al.*, 2009; Orrock *et al.*, 2010; Orrock and Witter, 2010). Of these, apparent competition in particular has been shown to be important in many systems (Schmitt,

1987; Settle and Wilson, 1990; Menge, 1995; Müller and Godfray, 1997; Chaneton and Bonsall, 2000; Östman and Ives, 2003; Oliver *et al.*, 2009; Blitzer and Welter, 2011; Long *et al.*, 2012), and particularly in host-parasitoid communities (Morris *et al.*, 2004, 2005; van Veen *et al.*, 2006; Cronin, 2007; Tack *et al.*, 2011; van Nouhuys and Kraft, 2012). Apparent competition occurs when two species that do not compete for resources are dynamically linked through a shared predator. Thus, an increase in density of one species causes a decrease in the abundance of the other, mediated by the shared predator (Holt, 1977). This can occur between generations, as the result of a numerical response by the predator, which experiences population growth sustained by one prey species, and this in turn leads it to exert greater predation pressure on the other prey species (Bonsall and Hassell, 1997). Apparent competition can also occur in the short-term, within the generation time of the interacting prey species, through an aggregative (Müller and Godfray, 1997) or a functional response (Long *et al.*, 2012). Both short-term and long-term apparent competition may operate in the same system over different temporal and spatial scales (Long *et al.*, 2012).

Studies focusing on pairs or small sets of species have been useful for identifying the mechanisms by which apparent competition may occur. However, in order to determine its importance at a community level, analysis of entire interaction networks is required to quantify interaction strengths among many species (van Veen *et al.*, 2006; Tack *et al.*, 2011). At the most basic level, species that share more predators within an interaction network should be involved in a larger number of apparent competitive interactions. Müller *et al.* (1999) articulated this concept for a bipartite food web by creating a measure of the potential for indirect interactions between any pair of species within a trophic level, based on the proportion of the total number of parasitoid individuals attacking one host species that were likely to have recruited from the other host species. This measure has been widely adopted to predict the potential for indirect interactions (Rott and Godfray, 2000; Schonrogge and Crawley, 2000; Valladares *et al.*, 2001; Lewis *et al.*, 2002; Barbosa *et al.*, 2007; Hirao and Murakami, 2008; Van Veen *et al.*, 2008; Nakamura and Kimura, 2009; Paniagua *et al.*, 2009; Alhmedi *et al.*, 2011), but its predictive success has rarely been tested, and never at a whole community level.

However, two experimental studies have shown that this information on shared parasitoids has great promise for predicting indirect interactions among herbivores. First, Morris *et al*. (2004) used a tropical host-parasitoid food web to identify two focal leaf-miner species (a beetle and a fly) that shared parasitoids with a range of other species. They experimentally lowered the abundance of the two focal species, and after several generations they found reduced parasitism rates and higher abundance of 12 other fly species that shared parasitoids with the focal fly species. Likewise, they observed reduced parasitism of a beetle species that shared parasitoids with the focal beetle species, exactly as predicted based on the quantitative food web.

In a similar test, Tack *et al.* (2012) used a quantitative food web to predict interactions among three species of leaf miner. They then experimentally increased the abundance of each in separate treatments. They found between-generation indirect interactions between some species as predicted, except that the effects were positive (i.e., apparent mutualistic; Holt, 1977) rather than negative (apparent competitive). Together these studies suggest that, at least in some cases, information on shared parasitoids can be used to successfully predict indirect interactions between species. However, the question remains as to whether information on shared parasitoids is predictive of all the apparent competitive/mutualistic interactions occurring across an entire host-parasitoid assemblage, given the wide range of proportions of shared parasitoids.

Finally, community-wide predictions of indirect interactions are made more difficult by the interconnections among adjacent habitats within landscapes. Global intensification of land use has created novel landscapes of managed and remnant natural habitats, and species movement among habitats may be an important determinant of resident species dynamics (Landis *et al.*, 2000; Holt and Hochberg, 2001; McCann *et al.*, 2005; Bianchi *et al.*, 2006; Rand *et al.*, 2006). Yet, it remains unknown whether apparent competition occurs across habitat edges, such that mobile predators dynamically couple prey populations in habitats on either side of an edge (McCann *et al.*, 2005; Tscharntke *et al.*, 2005; Rand *et al.*, 2006). If these predators drive widespread changes in abundance and population growth rates of prey in the new habitat, this process could be an important mechanism by which anthropogenic habitats impact the entire food web in adjacent natural habitats (Rand *et al.*, 2006).

In this study, I tested whether predator-mediated negative indirect interactions are an important mechanism structuring community-wide host-parasitoid interaction networks at the interface of native and plantation forests. Specifically, I asked the following questions:

1) Does apparent competition structure host-parasitoid assemblages to the extent that it is possible to use only quantitative food-web information on shared parasitoids, initial attack rates, and community-wide changes in host abundance to predict parasitism rates of all hosts within a community?

2) If this is the case, could it be that this predictability is due largely to the operation of intraspecific delayed density dependence, or do interspecific indirect effects indeed play a significant role?

3) Does apparent competition occur across habitat edges to the extent that it is possible to predict parasitism rates in one habitat based on changes in herbivore abundance in the adjacent habitat?

4) If so, does this cross-ecosystem effect occur asymmetrically, such that either **a)** fewer, or **b)** weaker cross-ecosystem indirect effects are exerted by hosts in one habitat on hosts in the other habitat than in the other direction?

3.3 Methods

3.3.1 Objective 1: Does apparent competition structure host-parasitoid assemblages within a habitat?

If apparent competition structures host-parasitoid assemblages, then it should be possible to predict parasitism rates of all species within a community based on three pieces of information: 1) a measure of the number (individuals per species) of shared parasitoids between a focal host species and all other hosts in the host-parasitoid assemblage; 2) the initial attack rate on the focal host species at a given site; and 3) the change in abundance since the initial attack rate was measured of all host species with which the focal host shares parasitoids. This is because if the abundance of a focal host is strongly affected by apparent competition with other host species, then changes in abundance of each other host species should affect the focal host to a degree proportional

to the number of parasitoids that the focal host shares with each other host. Conversely, if other interactions or stochastic processes are more important in structuring host-parasitoid assemblages than apparent competition, parasitism rates should not be predictable given only this information. I therefore tested the hypothesis that apparent competition structures host-parasitoid assemblages by collecting a measure of shared parasitism for each host pair, initial attack rates, and the changes in abundances of hosts, in order to calculate expected parasitism rates for all host species within the assemblage. I tested whether these expected parasitism rates significantly predicted the observed final parasitism rates. In order to answer my third objective: to determine whether apparent competition occurs across habitat edges, I conducted this study in the context of a habitat edge. However, first I address the question of whether or not apparent competition structures host-parasitoid assemblages within a habitat.

I obtained a host-by-host matrix of a 'regional' quantitative measure of shared parasitoids between each host pair. To do this I collected quantitative food web data at a set of 'training sites' over two seasons, and calculated the 'potential for indirect effects' between each pair of host species (see Eq.1). At a second set of 'validation sites', I measured initial parasitism rates of all host species, subsequent changes in abundance of all host species, and final parasitism rates of all host species, again by collecting quantitative food web data. I used separate sites for training and validating models of community-wide indirect effects because predictions robust enough to be useful for ecological applications should be able to be extrapolated to different locations within the same region. In order to ensure that host abundances did change significantly between initial and final parasitism rate assessments, I conducted a large-scale herbivore reduction at half of the validation sites.

3.3.1.1 Field site selection

I carried out this study at hard edges between plantation *Pinus radiata* forest and native southern beech (*Fuscospora* spp.) forest in the Nelson/Marlborough region of the South Island, New Zealand. I selected the two sets of forest edge sites (Fig. 3.1). At the eight training sites, I collected species interaction data to create a regional "metaweb" (a single web made up of all the webs from separate sites), from which to derive predictions

about the potential for indirect interactions based on shared parasitoids. The eight training sites were at least 2.7 km apart, and at least 1 km from any experimental validation site, and interactions were sampled seven times over two summer seasons (season 1: December 2009, January, February 2010; season 2: October, November 2010, January, February 2011). Sampling of the training sites in the second season was carried out by collaborator G. Peralta.

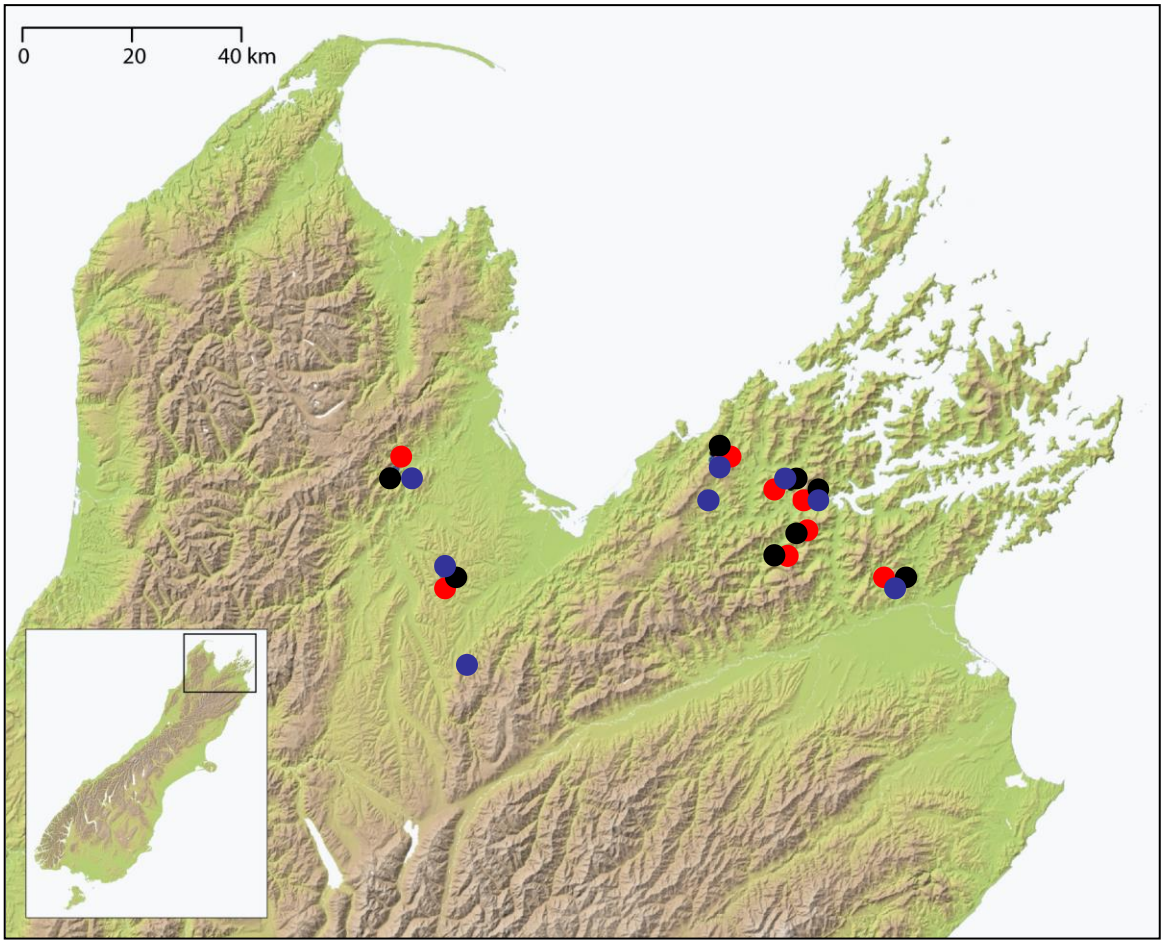

Figure 3.1. Locations of field sites in the Nelson/Marlborough region of South Island, New Zealand. Blue points represent 'training sites', and black and red points represent 'validation sites'. Black points are control sites, and red points are herbivore reduction treatment sites.

Toward the end of the model training period in early 2011, I experimentally reduced herbivore abundance in half of my validation sites, and these were each paired with a control site within eight spatial blocks. Spatial blocks were at least 2.7 km apart,

and within each block the pair of validation edge sites was at least 1 km apart, but not more than 2.7 km apart. Validation sites were sampled twice before the herbivore reduction treatment (October, November 2010) and twice after the herbivore reduction treatment (January, February 2011). The pine forests at my edges were between 17 and 28 years of age, with trees mature enough that the canopies were closed. I describe the understorey vegetation composition of the two forest types elsewhere (Chapter 2).

3.3.1.2 Sampling of species and interactions

Sampling procedures were the same at training and validation sites. To collect quantitative food-web data from which to assess indirect species interactions, I sampled lepidopteran larvae (caterpillars) and their parasitoids from the forests on both sides of the edge at each site. In each sampling round, I collected caterpillars at each site by establishing one 50 m transect in each forest type, 10 m from and parallel to the edge, which I designated as the last row of pine trees abutting the native forest. The 10 m distance was a compromise between a spatial scale over which parasitoids would be able to disperse, and a distance from the edge great enough that the vegetation was distinct from that of the adjacent habitat.

I sampled all vegetation within 1 m on either side and two vertical metres of each transect, by beating each plant and holding a sheet underneath to catch all of the caterpillars that were dislodged. I collected the caterpillars, keeping them separate according to their host plant. At ten points (i.e. at 5 m intervals along each transect), I sampled the lower canopy up to a height of 9 m, within an area of 1 m^2, by clipping all vegetation using an extendable pole with a clipper head on the end. If canopy foliage was not reachable at a designated clipping point, I clipped four or five branches (an approximately standard number of leaves) from the nearest reachable point. I beat all the clippings over large sheets and collected the caterpillars as for the understorey samples. When transect sampling yielded fewer than 50 individuals, I carried out extra sampling of vegetation on the non-edge side of the transect, and as near to the transect as possible, until either 50 caterpillars were found, or I had sampled for two person-hours. I used these extra sampling caterpillars to obtain more accurate estimates of per-capita

parasitism rate and to identify parasitoid-host interactions, but did not include them in any herbivore abundance calculations.

I housed the collected caterpillars individually, and reared each to adulthood or parasitoid emergence by feeding it foliage of the host plant on which it had been found, supplemented with artificial diet formulated for Beet Army Worm (Noctuidae) (Bio-Serv Entomology Custom Research Diets and Environmental Enrichment Products, New Jersey, USA). Adult parasitoids and moths were frozen and preserved in ethanol after emergence, and identified to species where possible using available taxonomic information (Huddleston, 1986; Austin, 1992; Walker, 1996; Berry, 1997; van Achterberg, 2004) and expert assistance (see Acknowledgements), and otherwise to morphospecies (hereafter species). Congeneric lepidopteran species that were indistinguishable as larvae had to be lumped, because when parasitoids emerged, larval morphology was my only means of identifying the host. However, there were only 13 such lumpings (Table S1.2), and these should not have affected the results of the study other than to create a more conservative assessment of whether indirect effects are important in structuring communities. This is because to lump two distinct species in this analysis would be to erroneously label some of the interspecific indirect effects on either of the lumped species as intraspecific effects. In addressing objective 2 (see section 3.3.2), I removed the contribution of intraspecific effects to the expected parasitism rates, so this lumping of species should only have made me less likely to find that expected parasitism rates significantly predicted observed parasitism rates.

Most of the parasitoid wasps collected were of undescribed species (Table S1.3). Therefore, in order to match males with females (which may have different morphology), I DNA-barcoded female specimens representing all of the observed morphological variation within each morphospecies, and all male specimens. To do this, I amplified and sequenced the Cytochrome c Oxidase subunit I (COI) region of the mitochondrial DNA (for detailed methods, see Appendix 3:A.3.1). I used Species Demarcation Tool v.1.0 (Muhire *et al.*, 2013) to calculate pair-wise similarity for each pair of aligned sequences, and used MUSCLE (Edgar, 2004) to re-align the sequences and cluster them based on similarity scores using a rooted neighbour-joining tree. I used a matrix of species by species similarity scores (Muhire *et al.*, 2013) to match unidentified males to female

morphospecies, and to lump within genera those morphospecies that sequence similarity suggested should be considered a single species. I did not set a strict percent similarity species demarcation criterion because I did not sequence all of my specimens, and therefore I could not use molecular information to split morphospecies. Rather, I lumped morphospecies based on obvious percent similarity groupings in the species by species similarity matrix. The lowest percent similarity between lumped morphospecies was 96.05%. Voucher specimens of parasitoid species have been deposited at the New Zealand Arthropod Collection, Landcare Research, Auckland, NZ, and the Museum of New Zealand Te Papa Tongarewa, Wellington, NZ, and COI sequences of barcoded wasps have been uploaded onto the BOLD Systems database (www.boldsystems.org; see Appendix 1: A.1.2 for tables of voucher specimens deposited).

3.3.1.3 Herbivore abundance manipulation

I attempted to generate large changes in herbivore abundance on the plantation side of the edge, with the expectation that this would reduce the *in situ* production of parasitoids and thereby affect parasitism rates, at least in the plantation, and possibly in the adjacent native forest as well. I applied a herbivore reduction treatment to one site in each block, leaving the other as a control. On 30 December, 2010 and again on 9 January, 2011, I sprayed an area of the plantation forest at each herbivore reduction site with Delfin WG (Certis, USA L.L.C.), a commercial formulation of *Bacillus thuringiensis* var. *kurstaki* - an organic, non-persistent pesticide. This bacterial strain kills larval Lepidoptera upon ingestion, but does not affect other insects. I sprayed an area of 2.5 ha at each herbivore reduction site (250 m along the edge, with the sampling transect at the centre, by 100 m into the interior of the pine forest), using a helicopter with micron air nozzles (droplet size roughly 100 microns). In each spray run I applied 4.5 kg/ha of Delfin WG, mixed with 0.125 L/ha of the wetting agent Du-Wet (Elliot Chemicals Ltd., Auckland, NZ). These amounts and timing were according to the manufacturers' instructions for maximal effectiveness, and comparable to amounts found to be maximally effective against lepidopteran pests (Tortricidae) in North American coniferous forests (Bauce *et al.*, 2004). As desired, the spray significantly reduced caterpillar abundance in the herbivore reduction plantation forests relative to the control

plantation forests (interaction effect Z = -3.18, p = 0.002, Table S3.1). Following the herbivore reduction in plantation forests we found only 17 % of the caterpillar abundance that we had found in the before-treatment collection, whereas at control sites we found 158 % of the caterpillar abundance from the before-treatment collection.

3.3.1.4 Data analysis

3.3.1.4.1 Regional quantitative measure of shared parasitoids

To generate a regional quantitative measure of shared parasitoids for each host species pair in the region, I created a quantitative food web for the region (the 'metaweb' from my training sites). I pooled the data from all the training sites across the seven collection rounds, in order to have the largest possible sample of interactions (i.e. the best resolution) from which to obtain information on shared parasitoids. I then used this regional metaweb to calculate a quantitative measure of shared parasitoids: d_{ij} (the dependence of parasitoids of host species *i* on host species *j*; Müller *et al.*, 1999). d_{ij} measures, for every pair of host species in a community, the proportion of parasitoids attacking host species *i* that recruited from host species *j* (Müller *et al.*, 1999):

$$d_{ij} = \sum_{k=1}^{P} \left[\frac{\propto_{ik}}{\sum_{l=1}^{P} \propto_{il}} \frac{\propto_{jk}}{\sum_{m=1}^{H} \propto_{mk}} \right] \quad (1)$$

where α is the link strength, *i* and *j* are a focal host species pair, *m* is an index of all host species from 1 to *H* (the total number of host species), *k* is a parasitoid species, and *l* is an index of all parasitoid species, from 1 to *P* (the total number of parasitoid species).

However, to extend this equation to multiple habitats, I indexed host species by habitat, such that, for example, species *i* in habitat *A* (e.g. plantation forest) would be treated as a separate species from species *i* in habitat *B* (e.g. native forest). Effectively, this expanded Equation 1 to explicitly consider two habitats, each containing hosts that share parasitoids which move freely between habitats. Thus, I calculated d_{iAjB}, the habitat-specific contribution to parasitism of host *i* by parasitoids of host *j*:

$$d_{i_A j_B} = \sum_{k=1}^{P} \left[\frac{\alpha_{i_A k}}{\sum_{l=1}^{P} \alpha_{i_A l}} \frac{\alpha_{j_B k}}{\sum_{m=1}^{H_q} \alpha_{m k}} \right] \quad (2)$$

where d_{iAjB} is the proportion of parasitoids attacking species *i* in habitat *A* that were reared from species *j* in habitat *B*. *A* is the habitat of host species *i*, *B* is the habitat of host species *j*, and *q* is the number of habitats over which all *m* host species are summed to get H_q, the total number of host species from the total pool of *q* habitats producing parasitoids. For all calculations with Equation 2 in this study, *q* includes both the native and plantation forests combined. All other variables are as defined in Equation 1.

The first part of Equation 2 represents the fraction of attacks by parasitoid species *k* on host species *i* in habitat *A* out of the total number of attacks by all of the *P* species of parasitoid on host *i* in habitat *A.* This is then multiplied by the number of parasitoids of species *k* that, in the same sampling period, were reared out of host species *j* in habitat *B*, divided by the total number of individuals of parasitoid species *k* that were reared out of all of the *H* host species in either of the habitats considered.

In the case where $A = B$, d_{iAjB} measures within-habitat shared parasitism, and when $A \neq B$, d_{iAjB} measures cross-habitat shared parasitism. However, in both of these cases $q = 2$, since even for parasitism within only one of the habitats, both habitats will contribute to the total pool of parasitoids. If the total pool of parasitoids occurs in only one habitat, Equation 2 simplifies to Equation 1 when $A = B$ and $q = 1$.) When $i = j$, d_{iAjB} measures the proportion of parasitoids attacking species *i* that recruit from species *i* in the same ($A = B$) or different ($A \neq B$) habitat.

3.3.1.4.2 Expected and observed parasitism rate calculation

I tested whether I could use knowledge of the proportions of shared parasitoids (d_{iAjB} values) between host species in my training metaweb, as well as quantitative food-web data from (pre-treatment) time *t* at my validation sites (i.e. 'initial' attack rates and host abundances), to predict parasitism rates at (post-treatment) time $t + 1$ at the validation sites, given known changes in host abundances. 'Parasitism rate' refers to the number of parasitism events divided by the number of hosts sampled. I first calculated the expected parasitism rate at time $t + 1$ of host species *i* in habitat *A*, $E_{iA(t+1)}$, using:

$$[E_{i_A}]_{t+1} = \sum_{j=1}^{H_q} \left[\left(\frac{d_{i_A j_B} \sum_{l=1}^{P} \alpha_{i_A l}}{n_{j_B}} \right)_t (n_{j_B})_{t+1} \right] \left[\frac{1}{n_{i_A}} \right]_{t+1} \quad (3)$$

where n is host abundance, t is a time step (sampling date), and all other variables are defined as in Equation 2. Here, when q = 2, B can take values of either habitat. When q = 1, B is limited to being either one habitat or the other (here plantation or native forest). That is, when q = 2, this equation calculates the expected parasitism rate of host i in habitat A based on potential apparent competition with hosts in the same *and* the adjacent habitat. When q = 1 it calculates the expected parasitism rate of host i in habitat A based on potential apparent competition with hosts *either* in plantation or in native forest. In both cases A can take values of either habitat. I calculated $d_{iAjB(t)}$ from the metaweb (transect plus extra sampling data) from my training sites, and $\alpha_{iAl(t)}$ (transect plus extra sampling data) and $n_{jB(t)}$ (transect data only) from my validation sites in the pre-herbivore-reduction samples at time t (in both reduction and control sites). I calculated $n_{jB(t+1)}$ and $n_{iA(t+1)}$ (transect data only) from the post-herbivore-reduction samples (also in both reduction and control sites). This equation calculates, for every host j in both habitats that shares parasitoids with host i in habitat A, the per host j attack rate on host i of parasitoids that were reared from host j, multiplied by the t + 1 abundance of species j. When summed over all H, this gives the expected number of attacks (not rate) on species i at time t + 1, which is then divided by the abundance of species i at time t + 1 to give the expected parasitism rate. In cases where more attacks were predicted than hosts were collected in the t + 1 collection, expected parasitism rates were greater than one. I kept these cases in my analysis because they could be made usable for any practical purpose by further sampling until the number of hosts collected was at least equal to the predicted number of attacks, and also because they increased the power in my hypothesis tests below.

Equation 3 is written such that the expected parasitism rate of host i increases in proportion to the abundance of host j. Thus, it assumes apparent competition between hosts that share parasitoids rather than apparent mutualism. A positive correlation between expected and observed parasitism rate would therefore suggest that apparent competition is the most important type of indirect interaction within the community,

whereas a negative correlation would suggest that apparent mutualism is the dominant type of indirect interaction.

For the entire herbivore assemblage, I tested whether this expected parasitism rate significantly predicted the observed parasitism rate of each host species *i* at time *t* + 1, $O_{iA(t+1)}$, which was calculated as:

$$[O_{i_A}]_{t+1} = \left[\frac{\sum_{l=1}^{P} \alpha_{i_A l}}{n_{i_A}}\right]_{t+1} \quad (4)$$

where all variables are as defined in equation 3.

3.3.1.4.3 Hypothesis testing

I first tested whether expected parasitism rate based on shared parasitoids from both habitats could predict observed parasitism rate. This was to determine whether parasitoid-mediated indirect effects structure attack rates across the entire host-parasitoid assemblage to the degree that quantitative food webs can be used to predict parasitism rates (Objective 1). This test assumed that one pool of parasitoids was shared between the two adjacent habitats, with a habitat term included in the model to determine whether violation of this assumption was masking a relationship between expected and observed parasitism rate. That is, the interaction between the habitat term and expected parasitism rate tested whether predictive power of expected parasitism rate depended on the habitat of host *i*, since the habitat edge might filter natural enemies in one direction, and therefore make parasitism rates in one habitat less predictable because of the cross-habitat contribution to the expected parasitism rate.

However, there were many expected parasitism rates of zero, resulting from small numbers of hosts collected for a given species at a given site. Given that zero-values of the expected parasitism rates may thus represent an absence of data rather than a true expected value of zero, expected parasitism rate may predict the occurrence (or not) of parasitism more poorly than it predicts the level of observed parasitism when it does occur. I thus ran two analyses. In the first, I tested if expected parasitism rate based on shared parasitoids from both habitats could predict whether an observed parasitism rate would be non-zero, i.e. whether parasitism at any level would be observed. To this end, I transformed observed parasitism rate, $O_{iA(t+1)}$, into a binary variable, with non-zero

observed parasitism rates all coded as 1. I used a generalized linear mixed model with a binomial distribution, in which the binary version of $O_{iA(t+1)}$ was predicted by $E_{iA(t+1)}$, habitat_A, and their interaction, and block plus site nested within block were included as random factors. $E_{iA(t+1)}$ was log transformed to achieve a more even distribution of values and improve linear model fit. To select the best model (here and for subsequent models), I began with the full model and sequentially dropped the interaction and then main effects, and at each step compared the Akaike's Information Criterion (AIC) values of the models with and without each dropped term, keeping the model with the lowest AIC value (Crawley, 2007). All general linear mixed models were conducted in the lme4 package (Bates, 2011) in R version 3.0.1 (R Core Team, 2013).

3.3.2 Objective 2: Are indirect effects that structure within-habitat host-parasitoid assemblages interspecific?

In the second analysis, I included only the cases in which parasitism was observed (i.e. non-zero), and tested whether expected parasitism rates significantly predicted the observed parasitism rates. I was most interested in whether the contribution to expected parasitism rate by interspecific and cross-habitat intraspecific indirect effects could predict observed parasitism rates, so I excluded within-habitat intraspecific contributions (i.e. cases where $i = j$ AND $A = B$) to the expected parasitism rate calculation in all models except where specified otherwise. (However, the qualitative results did not differ when intraspecific effects were included; see Appendix 3: A.3.3 for a re-analysis including within-habitat intraspecific effects).

In pursuit of Objectives 1 and 2, then, I first tested whether 'total' expected parasitism rate, based on shared parasitoids from both habitats (as above), could predict non-zero observed parasitism rate. I fitted a generalized linear mixed model with a binomial distribution, in which $O_{iA(t+1)}$ was the response variable and $E_{iA(t+1)}$, habitat_A, and their interaction were included as fixed predictors, and block plus site nested within block were included as random factors. A significant $E_{iA(t+1)}$*habitat_A interaction would mean that expected parasitism rate predicts observed parasitism rate with different success depending on the habitat of the focal host. I log-transformed $E_{iA(t+1)}$ to achieve a more even distribution of values and improve linear model fit.

3.3.3 Objective 3: Does apparent competition occur across habitat edges?

Next, I tested whether observed parasitism rates in both habitats could be predicted based on shared parasitoids in only one habitat, and whether predictions were only successful if they were derived from the same habitat in which parasitism was observed. This was to test whether predicted cross-habitat indirect effects are realized, or whether the habitat edge acts as a barrier. I set q equal to 1 in Equation 3, and used two separate models (one for q = plantation and one for q = native forest). I tested whether the observed parasitism rate for host i in habitat A could be predicted by expected parasitism rates calculated using quantitative food web information from only the plantation forest ($E_{iAjP(t+1)}$), or from only the native forest ($E_{iAjN(t+1)}$). In the first model, $O_{iA(t+1)}$ was predicted by $E_{iAjP(t+1)}$, the habitat type of the focal host (habitat_A), and the interaction between $E_{iAjP(t+1)}$ and habitat_A. In the second model, $O_{iA(t+1)}$ was predicted by $E_{iAjN(t+1)}$, habitat_A, and the interaction between $E_{iAjN(t+1)}$ and habitat_A. Block and site within block were included as random factors, and expected and observed parasitism rates were log-transformed to achieve a more even distribution of values and improve linear model fit.

Here, a significant interaction in the first model would mean that parasitism rates in the native forest and parasitism rates in the plantation forest were not equally well predicted by quantitative food-web data from the plantation forest. A significant interaction in the second model would mean that parasitism rates in the native forest and parasitism rates in the plantation forest were not equally well predicted by quantitative food-web data from the native forest. For example, in the first model, expected parasitism rate calculated from quantitative food web data from the plantation might better predict observed parasitism rate in the plantation than in the native forest. This could occur if the habitat edge filters parasitoids (Eycott *et al.*, 2012), such that predicted cross-edge interactions are not realized to the same extent as predicted within-habitat interactions. Conversely, expected parasitism rate calculated from quantitative food web data from the plantation might better predict observed parasitism rate in the native forest than in the plantation. This could result from cross-habitat intraspecific effects making a more significant contribution to predicted parasitism rates than within-habitat interspecific

effects (given that within-habitat intraspecific effects were excluded from the calculations of expected parasitism rate; see section 3.3.2 Objective 2).

3.3.4 Objective 4a: Do cross-ecosystem indirect effects occur asymmetrically in the number of predicted interactions that are realized?

Next, I tested whether cross-edge indirect interactions could be predicted equally in either direction. I re-ran the two models in which expected parasitism rate was derived from a single habitat (q = 1), this time including within-habitat intra-specific effects in the calculation of expected parasitism rates. In comparing these two models, if the interaction between expected parasitism rate and habitat_A was significant in one model, for example in the $E_{iajP(t+1)}$ model, but not the $E_{iajN(t+1)}$ model, this would mean that, depending on the signs of the coefficients, a greater number of the indirect effects predicted to be caused by hosts in one habitat on hosts in the adjacent habitat were realized than vice versa.

3.3.5 Objective 4b: Do cross-ecosystem indirect effects occur asymmetrically in strength?

Finally, I tested whether indirect effects were stronger in one direction or the other across habitats, and compared this to the within-habitat strengths of indirect effects. To do this, I tested whether d_{iAjB} was significantly different for host pairs depending on the habitats of the indirectly affected versus affecting hosts (habitat_{AB}). For this test, I used data from the metaweb sampled at training sites, since this was sampled over the largest time period, and would therefore include the largest sample of potential apparent competitive/mutualistic linkages. I used an ANOVA to test whether the magnitude of d_{iAjB} was related to the identities of A and B in habitat_{AB}, where habiat_{AB} could be PN, NN, NP, or PP.

3.4 Results

Transect plus extra sampling at my training sites yielded 8321 caterpillars. Of these, 2718 individuals from 68 distinct species in seven families were successfully

reared to moth or parasitoid emergence. These yielded 351 parasitism events by 43 species of Hymenoptera and Diptera parasitoids. These 351 parasitism events made up the data from which the training metaweb was constructed and d_{iAjB} was calculated in equation 3. The metaweb had a binary connectance of 0.056, which is within the range of connectances exhibited in published quantitative food webs (Dunne *et al.*, 2002).

Transect sampling at my validation sites yielded 5837 caterpillars that were identifiable to species level, and included 67 species. These made up the data from which I calculated all abundance terms (n) in equation 3. Of these caterpillars, 2067 were successfully reared to moth or parasitoid emergence, yielding 260 parasitism events by 35 species of parasitoid, in Hymenoptera, Diptera, and Nematoda. Extra sampling yielded an additional 1121 identifiable caterpillars, including four additional species, of which 405 were successfully reared to moth or parasitoid emergence, yielding 37 additional parasitism events, but no additional parasitoid species. The transect plus extra sampling total of 297 parasitism events made up the data from which $\alpha_{iAl(t)}$ was calculated in Equation 3.

I predicted the parasitism rate for each species within a validation site, when that species was found within the site in at least one sampling round. This resulted in 365 expected parasitism rate calculations. In the analysis of whether expected parasitism rate based on both habitats predicted the occurrence of parasitism (with $O_{iA(t+1)}$ as a binary response variable), I found that expected parasitism rate significantly predicted observed parasitism rate ($z = 2.98$, $p = 0.003$), and this did not depend on the habitat of the focal host (interaction between expected parasitism rate and $habitat_A$: $z = 1.78$, $p = 0.074$; Fig. 3.2, Table S3.2).

In the analysis of only non-zero observed parasitism rates, there were 17 cases in which a species within a validation site was parasitized in the 'after' collection. These made up the dataset for my test of how well expected parasitism rate predicted observed parasitism when parasitism did occur. Despite the fact that this low frequency of parasitism events in the after collection should lower predictive power, I found that total expected parasitism rate (based on both habitats) significantly predicted the magnitude of the observed (non-zero) parasitism rate ($z = 3.04$, $p = 0.002$; Fig. 3.3a). This did not depend on the habitat of the focal host (the interaction term was removed during model

selection). One of the points was an outlier (Fig. S3.1a), which I removed. However, the results did not change qualitatively when the outlier was included (Table S3.3).

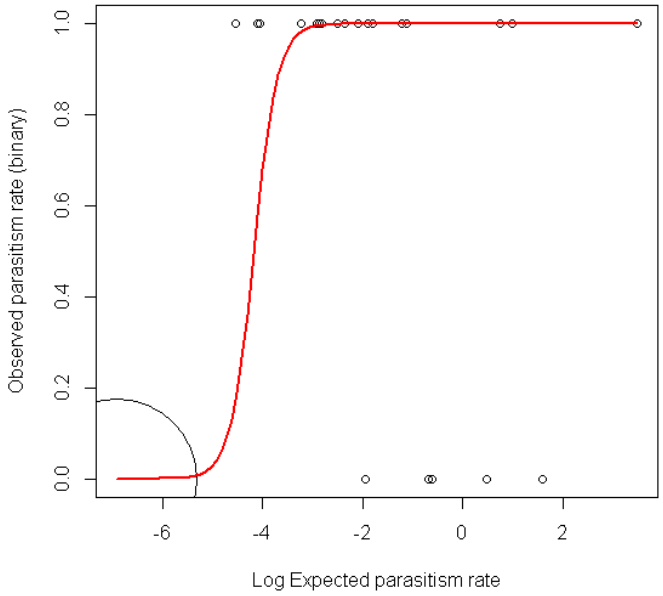

Figure 3.2. Expected parasitism rate significantly predicted the occurrence of parasitism (p = 0.003), and this did not depend on the habitat of the focal host (p = 0.074). Observed parasitism $O_{iA(t+1)}$ (as a binary response variable) is predicted by expected parasitism rate (log $E_{iA(t+1)}$ + 0.001). Data point size is proportional to the number of overlapping points. The trend line represents fitted values from the generalized linear mixed model in which observed parasitism rate was predicted by expected parasitism, habitat of the focal host, and their interaction, with block plus site within block as random factors.

When expected parasitism rates in both habitats were calculated based only on interactions occurring in native forest, the expected values $E_{iAjN(t+1)}$ significantly predicted the observed parasitism rate (z = 3.71, p = 0.0002; Fig. 3.3b). This did not depend on the habitat of the focal host (the interaction term was removed during model selection), nor did it change when the significant outlier (Fig. S3.1b) was included (Table S3.4).

When expected values for parasitism rates in both habitats were calculated based only on interactions occurring in plantation forest, $E_{iAjP(t+1)}$ significantly predicted the observed parasitism rate (z = 2.56, p = 0.010), and this did not depend on the habitat of

the focal host (the interaction term was removed during model selection; Fig. 3.3c, Table S3.5).

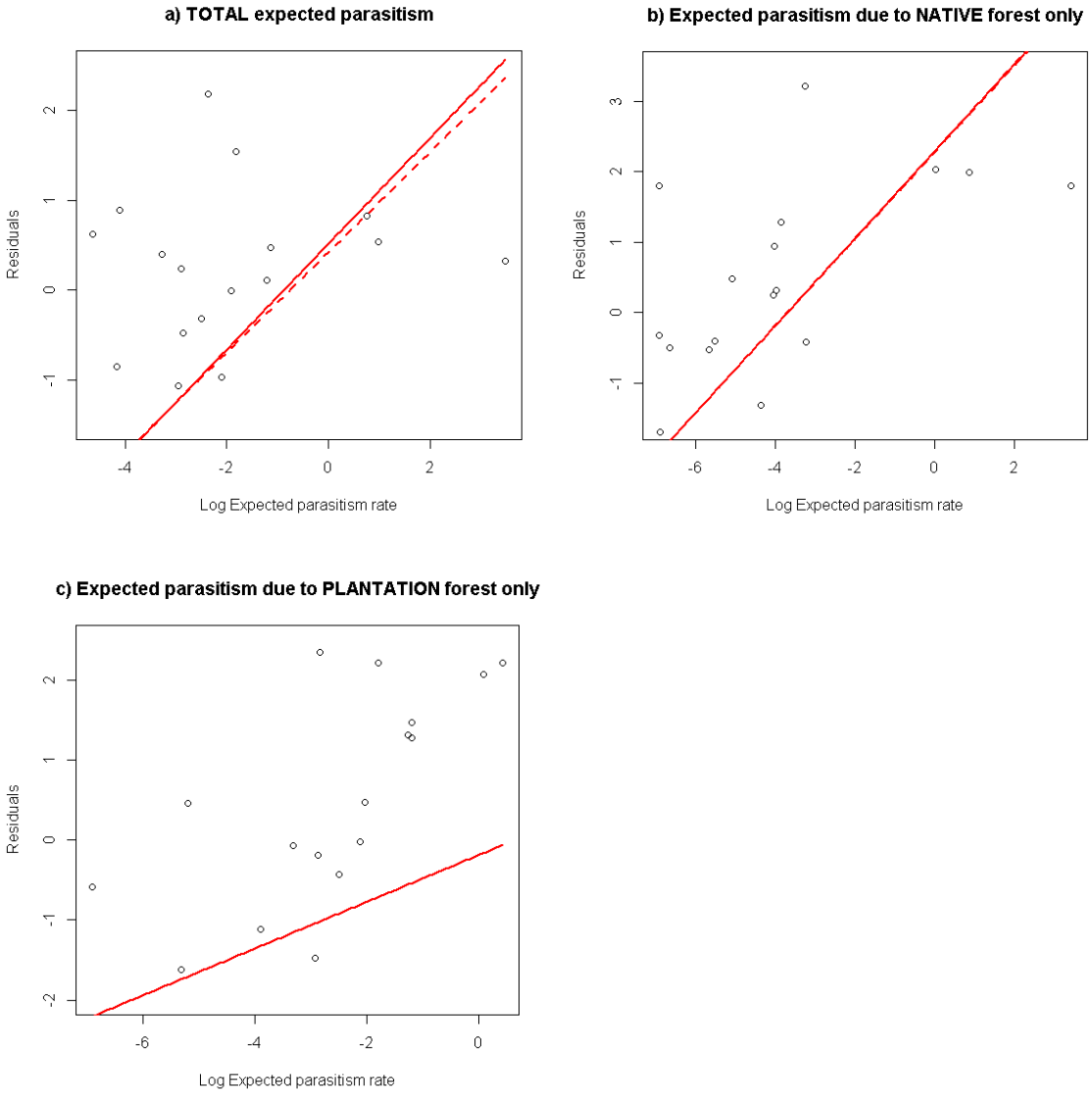

Figure 3.3. a) Total expected parasitism rate, log($E_{ia(t+1)}$), calculated from attacks expected due to hosts in native as well as plantation forest, b) expected parasitism rate due to hosts in native forest, log($E_{iajN(t+1)}$ +0.001), and c) expected parasitism rate due to hosts in plantation forest, log($E_{iajP(t+1)}$ +0.001), as a predictor of magnitude of residual observed (non-zero) parasitism rate, $O_{ia(t+1)}$, for hosts in native forest (n = 13) and plantation forest (n = 5). Plotted data are the residuals of a GLMM in which observed parasitism rate is predicted by site nested within block as random factors, to remove this source of variation from the relationship between observed and expected parasitism rate. Trend lines are the partial effects of expected parasitism rate from the GLMMs with binomial distribution, and site nested within block included as random factors. The dashed line in a) and

overlapping the solid line in b) are the trend line when the outlier (the furthest point to the right) is removed (see Fig. S3.1).

The results did not differ qualitatively for any of the analyses when within-habitat intraspecific effects were included in the calculations of expected parasitism rate (Tables S3.6-3.8). In all analyses, the correlations between expected and observed parasitism rates were positive, suggesting that overall, the indirect effects occurring were apparent competitive rather than apparent mutualistic.

I found that habitat_{AB} did not significantly predict d_{iAjB} ($F = 1.53$, $p = 0.206$). However, there was a non-significant trend toward hosts in plantation forest having greater potential apparent competitive effects on hosts in native forest than vice versa (Fig. S3.2).

3.5 Discussion

I found that apparent competitive effects occurred at the scale of an entire host-parasitoid assemblage, such that parasitism rates could be predicted based on quantitative food-web data. Following large experimental changes in herbivore abundance, observed parasitism rates were predicted by expected parasitism rates based on the proportion of parasitoids shared by each host pair, initial attack rates, and the change in abundance of each host species. The effects of food-web architecture on attack rates were predictable both within and across habitats, and predictions were accurate for interspecific effects or both inter- and intraspecific effects. I also found that apparent competition was more important than apparent mutualism in determining parasitism rates, as predicted by Müller *et al.* (1999), and found by Morris *et al.* (2004) for limited sets of species pairs. This is, to my knowledge, the first experimental whole-community test of the hypothesis that apparent competition can be a significant structuring force in communities, as well as the first community-scale demonstration of cross-habitat apparent competition.

In a long-term observational study, Kaartinen and Roslin (2013) found that the only detectable indirect effects resulting from natural population changes in a host-parasitoid community were intraspecific. Here, I explicitly excluded within-habitat

intraspecific effects from contributing to the expected parasitism rates, because this type of effect has been previously demonstrated (e.g., Tack *et al.*, 2011) and I wanted to determine whether interspecific indirect effects, as well as cross-habitat intraspecific indirect effects (which are important from a landscape management point of view), are important in structuring communities. Predictions of both interspecific effects (i.e. apparent competition) and intraspecific effects (i.e. predator spillover) of adjacent habitats based on parasitoid overlap were realized, such that the final attack rates were determined by the sum of both processes. In the models testing the expected parasitism rates calculated from single habitats as predictors of observed parasitism rate in both habitats, there were no expected-parasitism-rate*$habitat_A$ interactions, which means that interspecific indirect effects made at least as significant a contribution to apparent competition as did intraspecific cross-habitat effects.

Taken together, these results suggest that shared parasitoids can couple community dynamics across habitats, and this has implications for biological control strategies (e.g., Ito and Kondo, 2012), as well as for conservation of natural remnants. In land-sparing scenarios, in which production and conservation objectives are pursued in separate areas (Phalan *et al.*, 2011), spillover across habitat edges will still couple community dynamics between managed and natural habitats. This could have severe consequences for natural herbivore populations linked by shared predators to the extreme seasonal population outbreak (during growing season) and collapse (after harvest) dynamics of crop pests in production systems. Furthermore, the finding that parasitism rates can be predicted using food web data has potential applications in a wide range of areas, including biological control (Holt and Hochberg, 2001), predicting impacts of invasive species at a community level (Carvalheiro *et al.*, 2010), and predicting impacts of agriculturally-subsidized predators on food webs in adjacent natural areas (Rand *et al.*, 2006).

Cross-habitat apparent competition has been predicted to be a potentially important mechanism by which predator subsidies may affect entire food webs in recipient habitats (McCann *et al.*, 2005; Tscharntke *et al.*, 2005; Rand *et al.*, 2006). However, spillover from managed to natural habitats has scarcely been studied (Rand *et al.*, 2006; Blitzer *et al.*, 2012), either in terms of direct or indirect effects on the recipient

natural community, and never at a community scale. Empirically, proximity to a production system has been shown to increase predation pressure on aphid populations, as a result of spillover of agriculturally subsidized generalist coccinellid predators (Rand and Louda, 2006). However, it was not known whether more-specialized predators, such as parasitoids, might also mediate important cross-edge indirect effects (Rand *et al.*, 2006), because although some parasitoids are relatively generalized in host preference (e.g., Berry, 1997), others are much more trophically specialized, and are less likely to mediate functional changes in recipient habitats where host species or 'biotypes' differ from those in the source habitat (Rand and Tscharntke, 2007; Blitzer *et al.*, 2012).

I show here that a large assemblage of parasitoid species can mediate apparent competition between herbivore hosts in native and production forest, with indirect effects occurring in both directions. The extent to which predicted apparent competition was realized did not occur asymmetrically across the edge. Rather, observed parasitism rates for hosts in a focal habitat (whether native or plantation forest) could be predicted solely based on parasitoids shared with hosts in the adjacent habitat, initial attack rates, and changes in host abundances in the adjacent habitat. This suggests that both managed-to-natural and natural-to-managed-habitat spillover occur (as found in Chapter 2), and that herbivore populations on both sides of the habitat edge are dynamically linked by shared parasitoids. The magnitude of apparent competitive effects on hosts in one habitat from hosts in the other habitat was also not significantly asymmetrical. However, there was a trend toward hosts in plantation having a greater apparent competitive effect on hosts in native forest than vice versa, which is in line with the prediction that higher-productivity managed habitats will have a greater impact on lower-productivity natural habitats than vice versa (Rand *et al.*, 2006).

A caveat to the results presented here is that there was a small sample size of parasitized host individuals collected at validation sites in the 'after' collection, which resulted in few data points (Fig. 3.3) for testing how well expected parasitism rate predicted observed parasitism. However, despite this low power and the potential for differences in phenology across species to blur the strength of indirect effects, I found significant results. As well, the predicted parasitism rates for these individuals were based on the full metaweb of 351 interactions between 68 host species and 43 parasitoid

species, so expected parasitism rate for each species was based on community-wide interactions. These species were not selected based on predicted strength of indirect interactions, as in previous studies (Morris *et al.*, 2004; Tack *et al.*, 2011), and therefore represent a sample of host species unbiased by the aims of the study.

A further caveat is that these host-parasitoid assemblages were embedded in larger community networks, and in measuring parasitism rates rather than changes in abundance, I assume that parasitism rates by parasitoids do pertain to survival of hosts. Given that parasitoids almost always kill their hosts, parasitism does determine survival in terms of host-parasitoid interactions. As well, this approach prevented the possible confounding of resource competition and apparent competition in interpreting changes in population abundances. However, it is possible that, for example, high caterpillar predation by a generalist predator that ate parasitized and unparasitized individuals indiscriminately could alter caterpillar survival patterns significantly from those that might have been predicted by parasitism levels alone. Despite this possibility, this work is important in demonstrating apparent competition as a predictable structuring mechanism across a broad food-web compartment within the larger community. A future challenge will be to incorporate apparent competition and other indirect interaction mechanisms, as well as interactions between food-web compartments into the same predictive framework.

In conclusion, I provide evidence that apparent competition can drive community structure to such an extent that changes in herbivore abundance affect parasitism rates across habitats, and that these changes can be predictable based on knowledge of attack rates by shared parasitoids. This shows that apparent competition between species pairs, as demonstrated in so many systems (e.g. Settle and Wilson, 1990; Menge, 1995; Chaneton and Bonsall, 2000; Östman and Ives, 2003; Oliver *et al.*, 2009; Long *et al.*, 2012), does indeed scale up to influence community-wide interactions at the level of the food web. Important indirect interactions between species pairs are not isolated phenomena, but rather, are likely to be the norm between species that share predators. Furthermore, apparent competition can occur across a habitat edge, with effects acting in both directions: from managed to natural habitat, and from natural to managed habitat. This work suggests that communities within adjacent habitats in mosaic landscapes can

exert community-wide effects on one another, which is a process that should be considered in land management.

Chapter IV
Species traits can predict host and parasitoid contributions to apparent competition

4.1 Abstract

Accurate predictions of the community-wide effects of disturbance will depend on being able to predict not only direct, but also indirect effects. Apparent competition is an important type of indirect interaction that has been well demonstrated empirically, and recent progress has been made in predicting levels of apparent competition at the community level using quantitative food-web information. What is yet to be determined is where within a food web the strongest apparent competitive interactions will occur, and in which direction. Are there species traits, including trophic traits related to network position, that predispose species to being involved in strong apparent competition? I collected quantitative food-web data of plants, lepidopteran hosts, and their parasitoids from temperate forests, and tested whether sets of host and parasitoid traits can predict the potential for apparent competition between hosts, or a parasitoid's contribution to apparent competition, respectively. I found that greater differences in abundance between host species within a pair were associated with greater potential for the more abundant host to have strong apparent competitive effects on the less abundant host. In terms of network position, I found that apparent competitive effects 'flow outward'; that is, the greater the difference between host species in network position (their connectedness and closeness centrality), the greater will be the apparent competitive effect of the more connected or the more central host on the other. Host body size and host generality on plants did not significantly affect the potential for apparent competition. Parasitoid activity density, measured as the number of individuals of each parasitoid species captured in flight traps, significantly predicted a parasitoid's contribution to apparent competition in food webs, but parasitoid body size and attack rates (number of hosts parasitized) did not. These results could have great utility in the provision of alternative

hosts for conservation biological control, in predicting impacts of invasive species, and in modeling community-wide responses to disturbance.

4.2 Introduction

Indirect interactions are crucial in maintaining the stability of ecological networks in the face of disturbance (Montoya *et al.*, 2009), yet we know remarkably little about the mechanistic basis for indirect interactions or their cascading effects across ecological communities. Whereas direct interactions are easy to visualize within an interaction network, and relatively straight-forward to quantify (Memmott *et al.*, 1994; Laska and Wootton, 1998; Berlow *et al.*, 1999), indirect interaction strengths are more difficult to assign and the community-wide effect of any particular type of indirect interaction is more difficult to specify (Montoya *et al.*, 2009). Where these effects have been estimated, the strength of indirect interactions can be almost as large as that of direct interactions (Montoya *et al.*, 2003), and as important in influencing species abundances and distributions (O'Connor *et al.*, 2013).

Various mechanisms have been suggested to underpin density-mediated indirect interactions, including resource competition (Begon *et al.*, 1986), apparent competition (or mutualism; Holt, 1977), and trophic cascades (Knight *et al.*, 2005). It is likely that a multitude of indirect interaction mechanisms probably occur simultaneously (Sanders *et al.*, 2013), such that it is usually a net effect that is detectable (Yodzis, 1988; Montoya *et al.*, 2009). The pragmatic approach, therefore, has been to treat indirect interactions as a 'black box' and simply calculate residual indirect influences as community-wide net effects minus direct effects, thus avoiding mechanistic characterization of indirect effects (Laska and Wootton, 1998; O'Gorman *et al.*, 2010). However, in order to better predict and manage the effects of disturbance and species loss on ecological networks, there will need to be a greater mechanistic understanding of the causes and consequences of indirect effects within networks (Yodzis, 1988; Montoya *et al.*, 2009).

Of the many types of indirect interaction, apparent competition is known to be particularly important in many systems (Schmitt, 1987; Settle and Wilson, 1990; Menge, 1995; Müller and Godfray, 1997; Chaneton and Bonsall, 2000; Östman and Ives, 2003;

Oliver *et al.*, 2009; Blitzer and Welter, 2011; Long *et al.*, 2012), and especially in diverse phytophagous insect communities (Morris *et al.*, 2005; van Veen *et al.*, 2006; Cronin, 2007; Tack *et al.*, 2011; van Nouhuys and Kraft, 2012). Apparent competition occurs when a population increase of one species causes a population decrease in another species with which it does not interact directly, driven by the numerical or functional response of a shared predator (Holt, 1977). Many theoretical studies have concluded that apparent competition should be an important mechanism structuring communities (Holt, 1977, 1984; Holt and Kotler, 1987; Holt and Hochberg, 2001; Brassil and Abrams, 2004), and numerous empirical studies have demonstrated that apparent competition can be strong between pairs or small sets of focal species (e.g., Bonsall and Hassell, 1997; Müller and Godfray, 1997; Chaneton and Bonsall, 2000).

Müller *et al.* (1999) proposed that the potential for apparent competition could be predicted for any species pair within a community, based on the proportion of parasitoids attacking one species that had recruited from the other species. Further work experimentally validated Müller *et al.*'s (1999) measure of the potential for apparent competition, d_{ij}, for select species pairs within a community (Morris *et al.*, 2004; Tack *et al.*, 2011). However, Tack *et al.* (2011) also found that for some species pairs, indirect effects were apparent mutualistic, rather than apparent competitive. They also found that in some cases, predicted apparent competitive/mutualistic effects did not occur at all. This led to uncertainty as to how generally d_{ij} predicts indirect effects, and whether the dominant direction of effects is negative or positive (apparent competitive versus mutualistic). Recently, the predictive success of d_{ij}, was tested for all species pairs within a host-parasitoid assemblage, rather than for selected pairs only, using the same study system as described here in the present study. Müller *et al.*'s (1999) d_{ij} was shown to generally predict apparent competition (as a net effect, rather than apparent mutualism) for all species pairs within a community (Chapter 3).

Apparent competition, then, can structure entire communities, and can be predicted for all species pairs within a community based on quantitative information about shared consumers. What remains to be discovered are the determinants of non-random variation in indirect interaction strengths across the network. If the probability of apparent competition is not equally distributed across all species pairs that share a

predator within a network, then which network properties or species traits constrain the pathways by which apparent competition occurs?

Parasitoid overlap diagrams for quantitative food webs in a variety of systems suggest that the distribution of indirect interaction strengths is indeed likely to be highly asymmetrical across ecological networks (Müller *et al.*, 1999; Rott and Godfray, 2000; Valladares *et al.*, 2001; Lewis *et al.*, 2002; Barbosa *et al.*, 2007; Hirao and Murakami, 2008; Paniagua *et al.*, 2009; Alhmedi *et al.*, 2011), although little attempt has been made to discover determinants of this asymmetry. Understanding what intrinsic traits predispose species to be involved in or mediate apparent competition could have wide practical application in degraded systems. For example, it could allow better prediction of the impacts of invasive species on native species that share a common predator (Recart *et al.*, 2013), or it could represent a complementary tool for assessing likely non-target impacts of potential biological control agents (Barratt *et al.*, 2010).

A range of potential traits, such as trophic traits related to a species' position in the food web, may relate to indirect interaction strength. For example, prey species that are attacked by many predators have the potential to interact via apparent competition with all the other prey species used by those predators, and may be more likely to drive apparent competitive effects on less-well connected species than vice versa (Müller *et al.*, 1999). Furthermore, if a prey species is attacked by many predators that are very generalist in the prey they attack (i.e. if the prey occupies a central position in the direct interaction network), then that prey species may be more likely to cause apparent competitive effects on other species.

Lower-trophic-level interactions might also influence the distribution of indirect effects between prey species. Prey that feed on a diverse range of basal resources might be more likely to have apparent competitive effects on less generalist species for two reasons. First, more generalist prey species should be more ubiquitous in the environment, i.e. they can occur in different resource patches (Futuyma and Moreno, 1988; Southwood, 1988), as well as being more likely to be nearby a variety of other prey species, and are therefore more available to be converted into predator biomass that attacks those other prey. Second, generalist feeding decouples prey from the dynamics of any single resource species (Beddington *et al.*, 1978), so they are more likely to maintain

high and constant abundance in the face of spatial or temporal variability in any one of their resources, and thereby sustain high populations of their own natural enemies.

Beyond network position, there may be traits that predispose certain species to be involved in apparent competitive interactions more than others. For example, larger prey might typically transfer more energy to predators than small-bodied prey, thus making large prey more likely to drive apparent competitive effects, and small prey more likely to be influenced by them, for a given prey abundance. In a similar vein, more abundant prey species are likely to drive apparent competitive effects on less-abundant species, because more-abundant prey typically constitute greater total biomass available to be converted into predator biomass. However, the negative correlation between body size and abundance of species (Jonsson *et al.*, 2005; Woodward *et al.*, 2005) could lead these effects to cancel each other out if predatory feeding guilds were not size-structured, such that predators typically feed on similarly sized prey.

In addition, it is possible that certain predator traits may make some predators more likely than others to mediate apparent competition between prey species. McCann *et al.* (2005) showed that mobile predators can couple spatially compartmented food webs, and Rooney *et al.* (2006) emphasized that predator mobility allows coupling of fast and slow energy channels within food webs, which is important for stabilizing them. Similarly, a predator's propensity to move while foraging (e.g. its home range, search efficiency or dispersal capability) may predict the extent to which it couples prey in apparent competition. Body size may also be important, as it is correlated with mobility (Araújo *et al.*, 2004; Jetz *et al.*, 2004), and it determines per capita consumption rate (Ernest *et al.*, 2003; Brown *et al.*, 2004) and a predator's effect on prey populations (Emmerson and Raffaelli, 2004). Predator species' attack rates (a measure of abundance) may also determine the extent to which they mediate apparent competition (Müller *et al.*, 1999).

I therefore tested whether sets of host and parasitoid traits could predict host and parasitoid contribution to d_{ij}, the potential for apparent competition (Müller *et al.*, 1999), a statistic validated as corresponding to realized apparent competition in the temperate forest plant-Lepidoptera-parasitoid system considered here (Chapter 3). I hypothesized that host connectedness and centrality in the host-parasitoid network, generality on plant

resources, abundance, and body size would affect the potential for apparent competition between a host pair. I further hypothesized that parasitoid levels of movement, body size, and attack rates (a measure of abundance) would affect their contribution to the potential for apparent competition between host species.

4.3 Methods

4.3.1 Study system

I took advantage of two distinct datasets from the same study system. Both datasets included quantitative food webs collected at edges or edges and interiors of two forest types in the Nelson/Marlborough region, South Island, New Zealand. Since species composition did not differ by forest type or location, I pooled the data across forest type and location within a site. Each dataset consisted of samples from eight sites, and all sites were separated by at least 1 km (Fig. 4.1). Each site was a habitat edge between mature plantation *Pinus radiata* forest and *Fuscospora*-dominated native New Zealand forest.

In the first, a two-season dataset, I sampled at four locations per site: 10 m on either side of the edge (designated as the last row of planted *Pinus radiata* trees), and at the native and planted forest interiors (400-500 m towards each forest interior from the edge). Seven sampling rounds were conducted during two southern hemisphere summers: December 2009, January, February, October, and November 2010, and January and February 2011. This is identical to the 'training' data from Chapter 3, except that here I include data from forest interiors, not just edges. Collaborator G. Peralta conducted the sampling in the last four sampling rounds at these sites.

In the second, one-season dataset, I sampled at two locations per site: 10 m on either side of the edge, and conducted five sampling rounds: October and November 2010 and January, February, and March 2011. This is identical to the data from control sites in Chapter 2 and to the 'validation' dataset control sites in Chapter 3. Further details of the sites can be found in Chapter 2. I do not expect that any of the differences in the way the two datasets were collected would negate their combined use for the questions addressed in the current study. Nevertheless, I explicitly dealt with any potential bias due to the

different sampling periods and forest locations sampled between the two datasets using a random effect in all models.

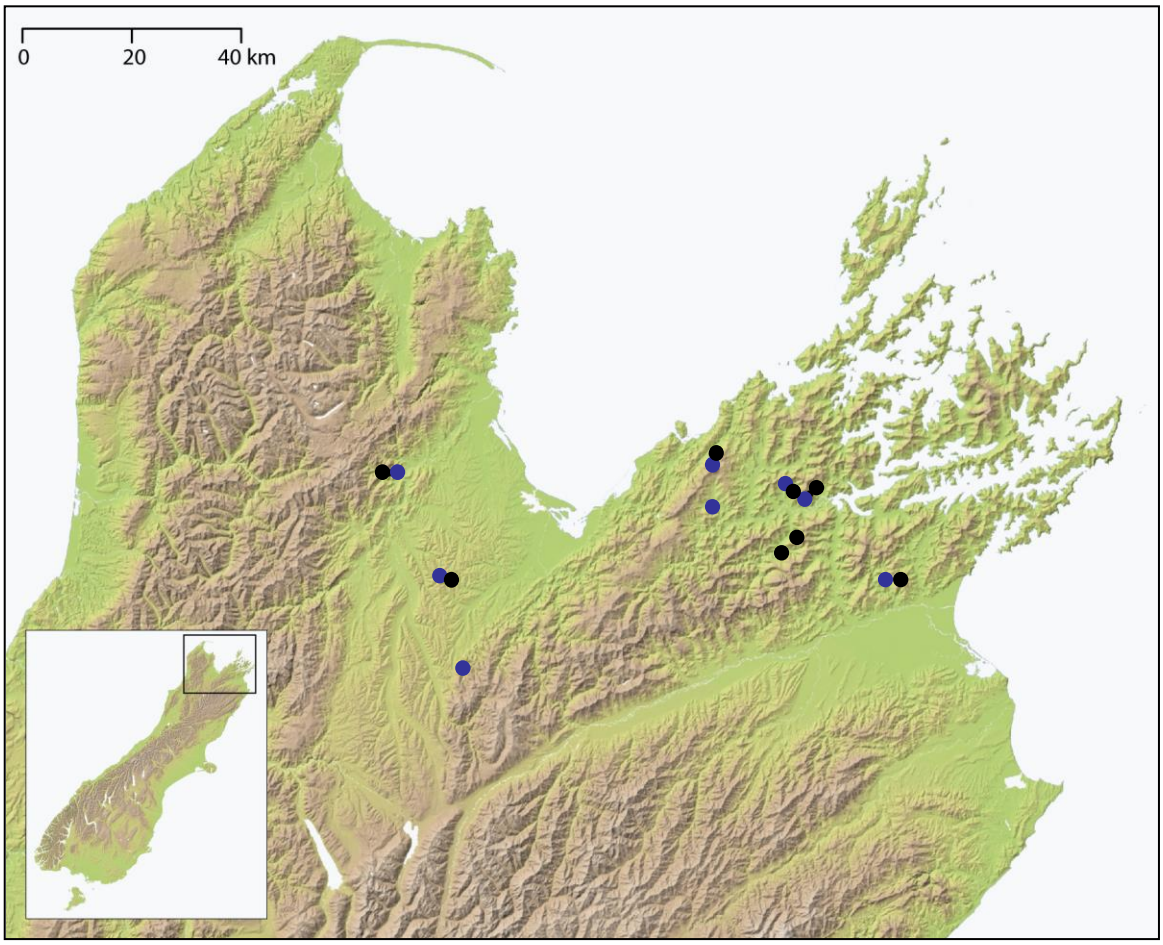

Figure 4.1. Locations of field sites. Blue points represent 'two-season dataset' sites, and black points represent 'one-season dataset' sites. All sites were separated by a distance of at least 1 km.

4.3.2 Sampling host and parasitoid abundance and interactions

Sampling techniques were identical for both datasets. At each sampling location, I beat all vegetation up to a height of 2 m along a 50 m x 2 m transect parallel to the forest edge. I collected all dislodged Lepidoptera larvae onto sheets held beneath the vegetation, and kept separate the larvae from each plant species. At ten points along each transect (each 5 m apart), I sampled the lower canopy by clipping all vegetation up to a height of 9 m within a 2 m x 1 m area, and beating the clippings over sheets to collect larvae.

Where there was no vegetation at a clipping point, I clipped four or five branches (a roughly standard number of leaves) from the nearest reachable canopy vegetation. When I collected fewer than 50 larvae on a transect, I sampled vegetation near the transect for up to an additional 2 person-hours or until I had found a total of 50 larvae. This extra sampling was to increase the resolution of the host-parasitoid food web, and extra-sampled larvae (and parasitoids) were used to produce the host parasitoid matrices for each dataset. However, only larvae from the transect were used as standardized samples of host and parasitoid abundance. I collected specimens of all plants sampled in order to identify them (using Dawson and Lucas, 2000; Eagle, 2006). Voucher specimens of sampled plants have been deposited in the University of Canterbury Herbarium, Christchurch, NZ (Table S1.1).

I identified the Lepidoptera larvae with the help of expert taxonomist J. Dugdale, and reared the collected larvae individually, each on the host plant on which it was found, combined with artificial diet formulated for Beet Army Worm (Noctuidae) (Bio-Serv Entomology Custom Research Diets and Environmental Enrichment Products, New Jersey, USA). Adult Lepidoptera or parasitoids that developed were frozen and preserved in ethanol or mounted for morphological identification (or confirmation of larval identifications in the case of the Lepidoptera), using (Huddleston, 1986; Austin, 1992; Walker, 1996; Berry, 1997; van Achterberg, 2004; Hoare *et al.*, 2011; Schnitzler and Ward, 2013) and expert assistance (see acknowledgements). Closely related congeneric Lepidoptera species that were indistinguishable as larvae had to be lumped in the quantitative food webs (see Table S1.2), since for parasitized larvae, larval morphology was my only means of identification.

Many of the parasitic Hymenoptera reared were of undescribed species (Table S1.3), and in many cases males could not be matched to females with any degree of certainty. I therefore identified them morphologically to morphospecies, and used DNA barcoding of at least two individuals per morphospecies to match males with females and lump morphospecies that grouped together based on DNA sequence similarity. I sequenced the Cytochrome c Oxidase subunit I (COI) region of the mitochondrial DNA (for detailed methods, see Appendix 3: A.3.1). I used Species Demarcation Tool v.1.0 (Muhire *et al.*, 2013) to calculate pair-wise similarity for each pair of aligned sequences,

and used MUSCLE (Edgar, 2004) to re-align the sequences and cluster them based on similarity scores using a rooted neighbour-joining tree. I used a matrix of species by species similarity scores (Muhire *et al.*, 2013) to group morphospecies with high percent sequence similarity into 'species'. I did not set a strict percent similarity species demarcation criterion because I did not sequence all of my specimens, and therefore I could not use molecular information to split morphospecies. Rather, I lumped morphospecies based on obvious percent similarity groupings in the species by species similarity matrix. The lowest percent similarity between lumped morphospecies was 96.05%. Voucher specimens of parasitoid species have been deposited at the Museum of New Zealand Te Papa Tongarewa, Wellington, NZ, and the New Zealand Arthropod Collection, Auckland, NZ, and COI sequences of all barcoded wasps have been uploaded onto BOLD Systems (www.boldsystems.org).

4.3.3 Sampling parasitoid movement

In order to measure movement levels of the parasitoid species mediating indirect effects in this system, I used malaise-style flight intercept traps at the one-season dataset sites. Each trap had a 1 m^2 collecting surface, with a hood that led into collection jars at the top, one on each side of the collecting sheet. At each site I hung four traps oriented with the collecting surface parallel to the forest edge (catching insects moving in either direction across the edge). Of the four traps, I hung two at 2 m above the ground, and two at 6-8 m above the ground. I opened the traps during the October 2010 collection, and collected the samples in November and December 2010, and January, February, March, and May 2011, leaving the traps open during the entire period between collections. I used propylene glycol as a killing and preservative agent in the traps, and upon collection, I sorted the samples, and identified parasitic Hymenoptera morphologically as described above. For logistical reasons I limited my trap sample analysis to hymenopteran parasitoids, and so excluded dipteran parasitoids from the study. However, hymenopteran parasitoids made up 85% and 92% of all parasitoids reared in the two-season and one-season datasets respectively, so they give a fair representation of trophic interactions in the community. I counted the total numbers trapped of each species of parasitoid that I had reared from Lepidoptera larvae in the quantitative food web sampling, and used this

as a measure of parasitoid movement levels, as in Macfadyen and Muller (2013). Because abundances of insects trapped in flight intercept traps may reflect both movement levels and density of the species present, I refer to this measure hereafter as 'activity density' (Thomas *et al.*, 1998). I distinguished movement by testing if there was still a residual effect of activity-density after accounting for a measure of parasitoid abundance ('attack rate', a measure of parasitoid larval abundance).

4.3.4 Measuring body size

In order to test whether body size of hosts or parasitoids affected their propensity to be involved in, or mediate, indirect interactions, I obtained mean body size estimates for all host and parasitoid species. Since I was not comparing body sizes between trophic levels, I used measures appropriate for Lepidoptera and Hymenoptera respectively. I obtained Lepidoptera body size estimates for Geometridae and Noctuidae by measuring the mean wing span of the scaled reference photos for each species on Hoare *et al.* (2011). For all other species I used the mean wing spans from Hudson (1928, 1939). Where species had been lumped together because of indistinguishable larvae, I used the mean of the wingspans of all the species that had been lumped into any one morphospecies.

Because there is no resource for New Zealand parasitoids equivalent to that for Lepidoptera, I measured parasitoid body size as the mean body length of my collected and mounted specimens. I used a microscope camera to photograph each specimen, and Adobe® Acrobat® XI to measure the distance from the front of the head between the antennae, to the tip of the abdomen. I measured up to ten specimens of each species, and used the mean body length per species.

4.3.5 Data analysis

I pooled the quantitative food-web data across all locations, sites, and collection rounds within each dataset, in order to create one 'metaweb' per dataset. This included the full range of interactions sampled, and thus the total potential for shared host use by parasitoids (and apparent competition). Previous work in the same system found that the potential for apparent competition calculated from such a metaweb could successfully

predict parasitism rates at a given host abundance (Chapter 3). From these metawebs, I calculated the potential for apparent competition between hosts, as well as the contribution of each parasitoid species to apparent competitive interactions between each host pair. I also calculated species-level food-web metrics to test as predictors of the potential for apparent competition.

4.3.6 Potential for apparent competition

I calculated the potential for apparent competition between two host species following Müller *et al.* (1999) as d_{ij}:

$$d_{ij} = \sum_k \left[\frac{\alpha_{ik}}{\sum_l \alpha_{il}} \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \right] \quad (1)$$

where *i* and *j* are host species, *k* is a focal parasitoid species, *l* represents the total number of parasitoid species, and *m* represents the total number of host species. α represents link strength, such that, α_{ik} is the number of attacks by individuals of parasitoid species *k* on individuals of host species *i*. This calculates, for all parasitoid species, the proportion of parasitoid individuals attacking host species *i* that recruited from host species *j*. I included only interspecific indirect interactions in all analyses (i.e. I left out all cases in which $i = j$, which is the diagonal of the interaction matrix).

To calculate the contribution of each parasitoid species *k* to d_{ij} I used a modification of Müller *et al.*'s (1999) d_{ij}, which I term d_{ijk}:

$$d_{ijk} = \frac{\alpha_{ik}}{\sum_l \alpha_{il}} \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \quad (2)$$

where all variables are as defined in equation (1). In order to focus on interspecific effects, I again excluded cases in which $i = j$.

4.3.7 Species-level network traits

In order to test whether certain host traits could predict whether those species were involved in indirect interactions, I calculated host species-level network traits. I calculated binary metrics as well as quantitative metrics in order to determine whether the binary metrics accorded with, and therefore could be used in place of, the quantitative

metrics. This would be beneficial, because the presence/absence of interactions is more easily measured (or determined from the literature) than is the strength/frequency of interactions. However, in interpreting the results I emphasize the quantitative metrics, since they include more information and are less susceptible to sampling biases (Banasek-Richter *et al.*, 2004).

From the host-parasitoid matrix produced from each dataset, I calculated binary and quantitative measures of the number of parasitoid species attacking each host species as 'normalized degree' and 'proportional generality' respectively (Dormann *et al.*, 2008), calculated for the herbivore level only. Normalized degree is the number of parasitoid species attacking a focal prey species, divided by the total number of parasitoid species, and proportional generality is a quantitative version of normalized degree (Dormann *et al.*, 2008). I calculated these metrics for herbivores again using the plant-herbivore matrix, as a measure of the trophic generality of herbivore species. As a measure of herbivore centrality in the network (i.e. whether they are connected to hubs or more peripheral), I calculated binary and quantitative measures of closeness centrality for herbivores, using the host-parasitoid matrix. Closeness centrality for a species is a measure of how easily energy could theoretically flow from that species to all other species in the network, through either direct or indirect pathways. That is, it is the inverse of the number of links between the focal species and all other species, with link strength accounted for in the quantitative version in that the "distance" decreases with stronger links to that species. In the case of bipartite networks, centrality can be calculated for a trophic level based on the unipartite projection of the bipartite network (Gomez *et al.*, 2011). In the unipartite projection, host species are linked when they share at least one parasitoid species. Therefore, centrality here measures the extent to which a host species i) shares parasitoids with many other hosts or ii) shares parasitoids with hosts that share parasitoids with many other hosts. I calculated all metrics using the *specieslevel()* function with log base 2 in the bipartite package (Dormann *et al.*, 2008) in R version 3.0.1 (R Core Team, 2013).

4.3.8 Hypothesis testing

I first tested whether host traits could predict the potential for indirect interactions between a host pair. I used two Gaussian generalized linear mixed models (GLMMs) in the lme4 package (Bates, 2011), one of which included the quantitative network metrics, and the other included the binary metrics. All traits, either network metrics (herbivore connectedness in the host-parasitoid and plant-host webs, and closeness centrality in the host-parasitoid web), or otherwise (abundance and body size), were entered into the models as ratios of the level of the trait for host *j* divided by the level of the trait for host *i*. Since this resulted in an uneven spread of values along the x-axis in all cases (because cases in which the value of the trait was greater for host *i* than for host *j* were constrained between 0 and 1), I log-transformed all trait metrics. In the first model, d_{ij} was the response variable, and the full model contained as predictors: host abundance, body size, proportional generality for the host-parasitoid web, proportional generality for the plant-host web, and quantitative closeness centrality. Host pair (*i-j* combination) and dataset were included as random factors to account for systematic variation between datasets or the non-independence of *ij* and *ji* for each host pair. In the second model, the response variable and random factors were the same, but the full model contained as predictors: host abundance, body size, normalized degree for the host-parasitoid web, normalized degree for the plant-host web, and binary closeness centrality. For both models, the assumptions of normality and homoscedasticity were violated, so d_{ij} was logit-transformed, after which the assumptions were met. To deal with the potential for multicollinearity given the large number of predictor variables modeled, I ran all subsets of the full model using maximum likelihood estimation, and selected as final the model with the lowest Akaike's Information Criterion (AIC) value. I then re-ran the final model using restricted maximum likelihood estimation, and used a Markov Chain Monte Carlo (MCMC) re-sampling procedure to estimate p-values on the final model, as recommended by Bolker *et al.* (2009). The MCMC procedure was carried out using the *pvals.fnc()* function in the languageR package (Baayen, 2010).

Next, I tested whether parasitoid traits could predict the contribution of a particular parasitoid species to apparent competition between host species. I used a GLMM with d_{ijk} as the response variable, logit-transformed to meet assumptions of

normality and homoscedasticity. I entered as predictors parasitoid species body size, activity density (i.e. the total number collected in flight intercept traps throughout the season in the one-season dataset, with values extrapolated to the same species in the two-season dataset as well), and attack rate (as a measure of abundance, i.e. number of parasitoids reared from hosts in each dataset). I included parasitoid identity nested within dataset and host pair identity nested within dataset as random factors to account for the non-independence of multiple measures from the same host pair or parasitoid species within each dataset. I used the same model selection and p-value estimation procedure as for the host trait models.

4.4 Results

At my two-season dataset sites, I sampled 78 species of plant, collecting 17,171 lepidopteran herbivore larvae. Of these, 5,737 herbivore individuals from 89 species were successfully reared to moth or parasitoid emergence, yielding 719 parasitism events by 54 species of parasitoid, 85% in the order Hymenoptera. At my one-season dataset sites, I sampled 69 species of plant, collecting 4,791 lepidopteran larvae. Of these, 1,551 herbivore individuals from 51 species were successfully reared to moth or parasitoid emergence, yielding 175 parasitism events by 27 species of parasitoid, 92% in the order Hymenoptera. The two-season dataset host-parasitoid metaweb had a connectance of 0.076, and the one-season dataset host-parasitoid metaweb had a connectance of 0.099 (as calculated by the *networklevel()* function in the bipartite package; Dormann *et al.*, 2008). These are within the range of connectances exhibited in published quantitative food webs (Dunne *et al.*, 2002).

In the model with quantitative metrics, I found that host abundance, proportional generality for the host-parasitoid web, and closeness centrality were significant positive predictors of the magnitude of d_{ij}, the potential for apparent competition (abundance: t = 5.48, $p_{MCMC} < 0.001$; proportional generality: t = 2.60, $p_{MCMC} = 0.013$; closeness centrality: t = 5.99, $p_{MCMC} < 0.001$; Fig. 4.2a,c,e, Table S4.1). Proportional generality for the plant-herbivore web and body size were not significant, and did not remain in the final model. Because the predictors were entered into the models as ratios, these results

mean that higher host body size, higher number of parasitoid species attacking a host species, or greater centrality of host species *j* relative to that of host species *i*, were associated with a greater potential apparent competitive effect of species *j* on *i*.

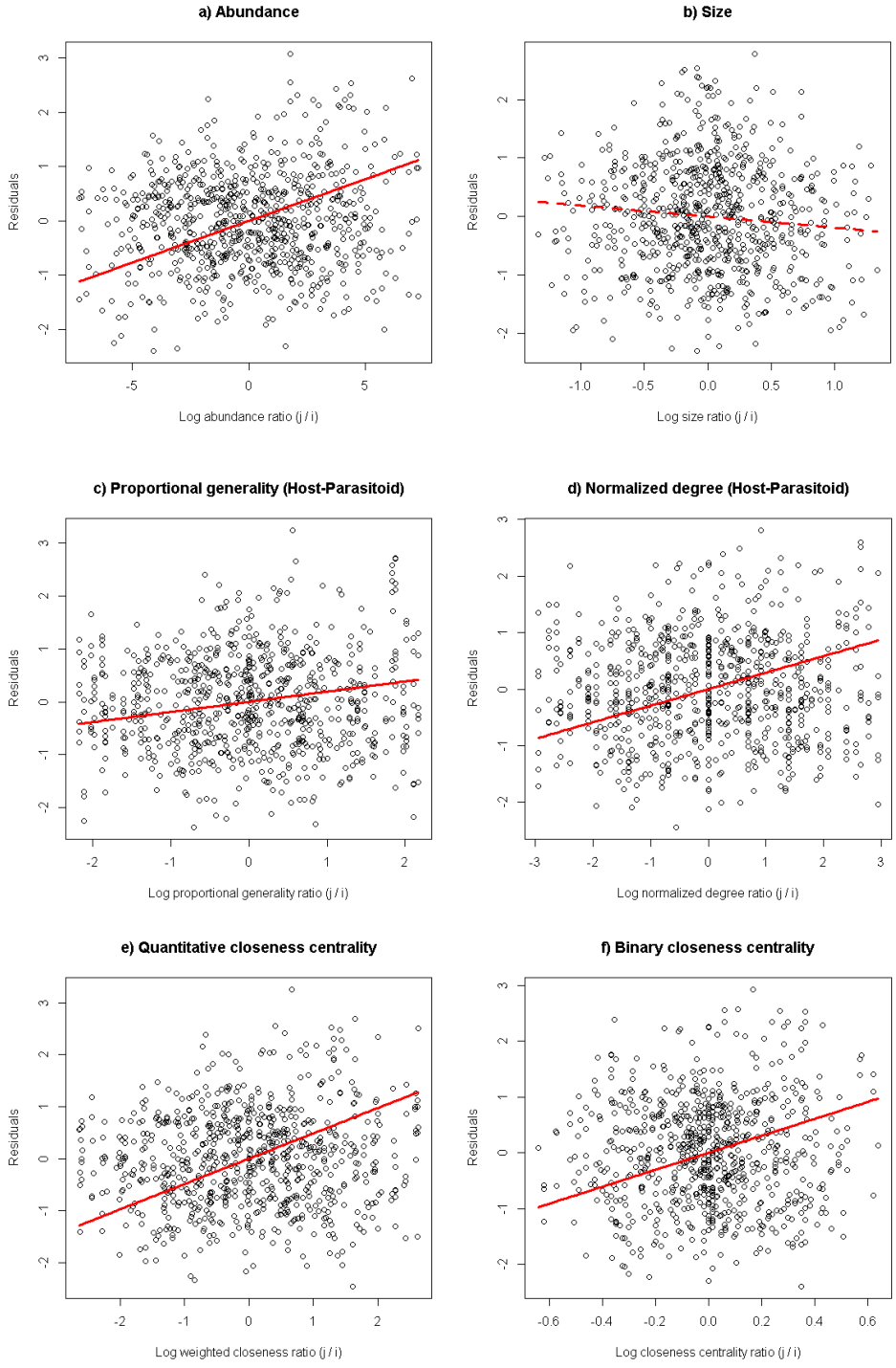

Figure 4.2. Relationships between the potential for apparent competition, d_{ij}, where host *j* affects host *i*, and the ratio (*j*/*i*) of various traits. Data plotted are the focal

predictor variable versus the residuals of the final model predicting d_{ij}, run excluding that predictor variable, in order to visualize the relationship between the focal predictor and d_{ij}, without the effects of the other predictors. Trend lines are the partial regression coefficient from the final model for the predictor variable. The dotted line in b) indicates a non-significant trend.

In the model with binary measures (normalized degree for the host-parasitoid web, normalized degree for the plant-host web, and closeness centrality), body size was retained in the model, but the main effect was not significant (Fig. 4.2b, Table S4.2). All the main effects were similar to those for the model with quantitative metrics, and the plots showed the same pattern as for the quantitative measures (Fig. 4.2d,f). However, there were several two-way and three-way interactions, as well as a four-way interaction between abundance, body size, closeness centrality, and normalized degree for the host-parasitoid web (t = 2.90, p_{MCMC} = 0.002; Table S4.2). Given that quantitative predictors are thought to be more accurate than binary predictors (Banasek-Richter *et al.*, 2004), and that there were no significant interactions in the model with quantitative metrics, I describe these interactions in the supplement (Appendix 4: *A.4.2*).

Of the parasitoid traits, only parasitoid movement, expressed as activity density, significantly predicted the contribution of a parasitoid species to apparent competitive interactions between host pairs (Table 4.1).

Table 4.1. Coefficients from the best-fitting model testing whether parasitoid traits can predict a parasitoid species' contribution to the potential for apparent competition, logit-transformed d_{ijk}. The full model contained the fixed predictors parasitoid length, abundance (measured as number reared out of host larvae), and activity density (all log-transformed), and all interactions. Host pair identity nested within dataset, and parasitoid species nested within dataset were included as random factors. P_{MCMC}-values in bold are significant at $\alpha = 0.05$.

Fixed effects:	Estimate	Standard Error	t-value	p_{MCMC}-value
Intercept	-4.0364	0.6725	-6.00	0.0870
Size	0.2620	0.1159	2.26	0.2062
Abundance	0.0270	0.0227	1.19	0.6002
Activity density	0.0346	0.0114	3.03	**0.0042**
Size:Abundance	-0.0126	0.0065	-1.94	0.1970

4.5 Discussion

I found that species traits, including network-related traits of host species, could significantly predict the potential for apparent competition across a host-parasitoid community. Apparent competition is known theoretically and empirically to be an important mechanism by which species indirectly interact (Holt, 1977; Holt and Kotler, 1987; Settle and Wilson, 1990; Bonsall and Hassell, 1997; Morris *et al.*, 2004; van Veen *et al.*, 2006). However, until now prediction of the strength of apparent competition between host species has required calculation of the proportion of shared parasitoids between a pair of hosts (Müller *et al.*, 1999). This approach necessitates collecting quantitative food-web data for a community, which is laborious, and in some systems virtually impossible because of the difficulty in accurately quantifying interaction strengths. My results show that normalized degree of host-parasitoid webs and closeness centrality calculated from binary food-web data were sufficient to predict the potential for apparent competition in a way consistent with the respective quantitative metrics. This suggests that the strength of apparent competition between prey species may be predictable even in systems from which quantitative food webs have not traditionally

been made, and that even knowledge of the parasitoid species that attack two herbivore species (which can be obtained from the literature) could be used to predict apparent competition between them. However, it remains to be tested how well binary network traits predict interactions in systems in which predator-prey relationships are less tightly co-evolved than in host-parasitoid systems (Scotti *et al.*, 2007).

Theoretical work on the stability of ecological networks in the face of disturbance has found that quantifying the strength of indirect interactions is necessary in order to make successful predictions (Yodzis, 1988). However, ecologists have struggled to determine interaction strengths associated with particular indirect interaction mechanisms (Montoya *et al.*, 2009). I found that prey species that are more connected by predators, or more central in the network, tend to exert strong apparent competitive effects on less connected and less central prey species respectively, and that the potential indirect interaction strength increases as the difference in network position increases between host species. This represents a first step in understanding the tangle of indirect interactions that can obscure the outcomes of direct interactions in food webs.

My results were as hypothesized based on Müller *et al.*'s (1999) d_{ij}, since for any species pair, a more connected host had a greater apparent competitive effect on the less connected host, assuming they shared at least one parasitoid. However, such a correlation would not occur over all species within a network if less connected species were usually attacked by specialists, so this finding is not obvious from the calculation of d_{ij} alone.

I further found that, regardless of network position, host abundance could predict the potential for apparent competition. Specifically, more-abundant species had greater potential apparent competitive effects on less-abundant species. This relationship seems intuitive, because within a host pair, the host species that produces more parasitoid species and individuals is likely to have a higher apparent competitive effect on the host species that is not attacked by as many parasitoids (Müller *et al.*, 1999). More abundant hosts are likely to be more highly parasitized, because of the potential for positive density-dependent predation (Ishii and Shimada, 2012) in the short term, and predator adaptation to capitalize on abundant resources (Brown and Wilson, 1956) in the long term. However, despite these mechanisms being recognized to occur in the few systems investigated (Hughes and Croy, 1993; Pfennig *et al.*, 2006), there is little empirical

information as to whether they are the norm across a community. From an energy flow perspective, species for which there is more biomass available to parasitoids, either because of high abundance or high body mass, should produce more parasitoids. The abundance result therefore matches theoretical expectations, but it is interesting that body size is not a similarly useful predictor. It could be that parasitoids often specialize on hosts of certain body size (or traits that correlate with body size), and this could be the reason why there is no pattern of large hosts exerting strong apparent competitive effects on smaller hosts. Alternatively, it is also possible that the abundance effect could result more from a correlation between high abundance and ubiquity in the environment, rather than from a total biomass effect.

However, I found that host generality on plants (herbivore connectedness in the plant-host webs), another measure of host ubiquity in the environment, did not significantly predict the potential for apparent competition. This accords with a study which found that increasing patch size of a prey's host plants did not increase parasitoid attack rates (Sheehan and Shelton, 1989). This could mean that host location is not the factor limiting parasitism events in this system, particularly if parasitoids disperse well. It is therefore likely that parasitoid host-use specialization, rather than encounter rate restricts parasitoids from using the most spatially ubiquitous prey species.

My results showed that one parasitoid trait significantly predicted parasitoid contribution to apparent competition: higher levels of parasitoid activity density were associated with greater parasitoid contribution to the potential for apparent competition between a host pair. Although activity density is a combination of parasitoid abundance and movement, activity density was a significant predictor of a parasitoid species' contribution to apparent competition even after the effect of abundance (measured as attack rate, i.e. number of parasitoids of each species reared) was removed, which suggests that parasitoid movement is positively correlated with contribution to apparent competition. This is an empirical confirmation of theoretical work suggesting that mobile predators couple distinct energy channels (Rooney *et al.*, 2006) and that predator mobility is important in coupling spatially separated food web compartments (McCann *et al.*, 2005). Because the parasitoid species that were captured most often in flight traps were

those most likely to mediate apparent competition, they provided dynamic coupling of potentially very separate energy pathways within the food web.

There was also a non-significant trend toward larger parasitoid species contributing more to apparent competition. This was after the effects of activity density were removed, and thus represents the effect of body size over and above the potential correlation between body size and mobility in Hymenoptera (e.g. Araújo *et al.*, 2004). In non-host-parasitoid food webs, body size has been found to correlate positively with interaction strength (Emmerson and Raffaelli, 2004), and this may be the case in host-parasitoid webs as well. Parasitoid abundance (the number reared out of host larvae) did not significantly predict a parasitoid species' contribution to apparent competition, possibly because abundant parasitoid species may not always have been generalist enough to mediate apparent competition, and they may have only exerted strong attack rates on few hosts.

The identification of at least one parasitoid trait and three host traits that allow prediction of the potential for apparent competition between hosts, regardless of host pair identity and other food web information, could be very useful in a variety of practical scenarios. For example, in classical biological control, there are still no tools available for assessing potential non-target impacts via indirect interactions (Barratt *et al.*, 2010), despite the recognition that these are likely common (Alhmedi *et al.*, 2011; Simberloff, 2012; Tylianakis and Binzer, 2013). The parasitoid and host traits found to be significant here are at least a starting point and could be included in probabilistic risk assessment approaches (Wright *et al.*, 2005). There are also biological control situations in which introducing an apparent competitor and a predator to cause apparent competition can improve the desired biological control outcome (Karban *et al.*, 1994). The results of this study represent a starting point from which to be able to plan such outcomes. Predicting the indirect impacts of invasive species (e.g., Recart *et al.*, 2013), and of spillover of organisms across habitat edges (Rand *et al.*, 2006) are other scenarios in which it will be critical to understand how species traits correlate with the potential for apparent competition, within and across habitats.

In this study, rather than a direct measure of realized apparent competition, I used Müller *et al.*'s d_{ij} (1999), the potential for indirect interactions, which includes apparent

mutualism as well as apparent competition (Tack *et al.*, 2011). However, previous experimental work in this system found that d_{ij} successfully predicted negative indirect interactions (i.e. apparent competition rather than mutualism) at a community scale (Chapter 2), so I interpret d_{ij} as predicting the potential for apparent competition rather than apparent mutualism, and have confidence that d_{ij} actually does predict true apparent competition in this system. It remains to be tested to what degree apparent mutualism confounds apparent competition in other systems at the level of entire communities, and thus whether traits that may correlate with d_{ij} in other systems also correlate with realized apparent competition.

Many separate lines of ecological research have recognized the importance of indirect interactions in structuring communities (van Veen *et al.*, 2006; Montoya *et al.*, 2009; Simberloff, 2012), and each has suffered from a lack of tools with which to predict the outcome of indirect interactions. The traits identified here could be used to improve predictions about the indirect impacts of invasive species, biological control agents, and spatially subsidized predators and prey spilling across habitat edges, as well as to improve predictions about how complex ecological networks will respond to disturbance.

Chapter V
Discussion

5.1 Effects of a productivity gradient between adjacent habitats

This thesis demonstrates that adjacent managed and natural habitats are linked through bi-directional spillover of natural enemies, and that this dynamically couples herbivore populations across habitats. Furthermore, these results support the hypothesis that there is a net spillover of natural enemies in the managed-to-natural direction (Rand *et al.*, 2006), at least in part driven by bottom-up differences in productivity.

As predicted, I found in Chapter 2 that there was a net flow of natural enemies from exotic production forest to native New Zealand temperate forest. *Pinus radiata* plantation is estimated to be roughly twice as productive as native New Zealand forest (Tate *et al.*, 1997; Trotter *et al.*, 2005), in keeping with the global trend that managed land is often more productive than nearby natural land (Field *et al.*, 1998). In the case of the most generalist predators considered, *Vespula* species wasps, I experimentally confirmed that the magnitude of spillover in the managed-to-natural direction depended on herbivore abundance.

Given this asymmetrical spillover across the habitat edge, I expected that the magnitudes of the direct and indirect effects of natural enemies would be similarly asymmetrical across the two habitat types (Rand *et al.*, 2006). This was likely the case for the generalist *Vespula* species, which are known to exert strong density-dependent direct and indirect effects on other species and ecosystem functions in New Zealand beech forest (Barr *et al.*, 1996; Beggs and Rees, 1999; Elliott *et al.*, 2010; Wardle *et al.*, 2010; Beggs *et al.*, 2011). For the more specialist predators (parasitoids), there was no evidence that the magnitude of cross-edge direct effects (i.e. parasitism rates) was linked to herbivore abundance (Chapter 2). However, this may have been an artifact of my treatment, if the herbivore reduction treatment was not as effective at killing sheltered host species (from which parasitoids may primarily recruit) as it was at killing larvae consumed by generalist predators. If this were the case, this experimental bias would also have affected the detectability of asymmetrical indirect interactions. Despite this, in

Chapter 3 I found a non-significant trend toward greater apparent competitive effects of hosts in plantation on hosts in native forest than vice versa at control sites.

The roughly two-fold productivity difference between forest types considered here was relatively small compared with other adjacent managed and natural habitats, such as between cropland and prairie (five-fold), or cropland and forest (25-fold; Ovington *et al.*, 1963). The only management of the plantation forests considered here is pruning and thinning, without nutrient inputs, and their higher productivity is due to the fast-growing tree species, for which the rotation time is only 28 years. It might be expected that, all else being equal, greater productivity differences between habitats would result in greater asymmetry in spillover and greater asymmetry in magnitudes of cross-edge direct and indirect effects (Oksanen, 1990; Oksanen *et al.*, 1992; Rand *et al.*, 2006). For example, we might expect to see spillover and associated cross-habitat interactions that are even more asymmetrical between production land with intensive fertilization of a fast-growing crop, and adjacent native vegetation, if productivity is the primary factor determining net insect movement.

5.2 Directional natural enemy movement between habitats

A range of factors in addition to productivity may influence levels of insect movement. Movement of organisms between habitat types may be affected by their densities (Turchin, 1989; Ries and Debinski, 2001; Enfjäll and Leimar, 2005), as well as by differences in resource quantity and quality (Schultz *et al.*, 2012), predation pressure (Stevens *et al.*, 2006), and physical structure (Cadenasso and Pickett, 2001; Ricketts, 2001; Ries and Debinski, 2001; Jackson *et al.*, 2009; Kuefler *et al.*, 2010; Eycott *et al.*, 2012) between the habitats. The result in Chapter 2, that natural enemies showed net movement from plantation forest to native forest, suggests that enemy density, driven by habitat productivity and resulting herbivore densities, may drive spillover in this system. *Vespula* species in New Zealand are also known to derive important carbohydrate resources from the beech honeydew abundant in the native forest (Beggs *et al.*, 2011). Conversely, protein resources may be more abundant in plantation forest, given its higher primary productivity. As well, the soft, loose soil common in mature plantation pine forests relative to native forest may provide better nesting sites.

Combined, these resource requirements mean that *Vespula* wasps are generalist species that clearly derive important resources from both habitat types, and as a result may be more abundant at edges than at forest interiors. However, the fact that I found a net spillover of *Vespula* species wasps from plantation to native forest suggests that nest densities are higher in the plantation side of the edge than in the native forest side of the edge. This could be because of greater nest site availability rather than because of greater food availability in the plantation relative to the native forest. However, the result that *Vespula* species spillover from plantation to native forest decreased significantly following herbivore reduction suggests that the asymmetrical spillover is driven by a gradient of prey availability.

Structural differences between neighbouring habitats have also been shown to limit insect movement between habitats (e.g., Ricketts, 2001; Ries *et al.*, 2004). Given that the parasitoid guild considered here included 35-46 different species (depending on which set of sites in Chapter 3, or which dataset in Chapter 4 is considered), it was likely that at least some of these species would find the structural contrast or abiotic differences associated with the plantation-native edge to be a barrier to movement (Ries and Debinski, 2001). Plantation forests were often more open in the understorey and canopy levels than the adjacent native forests, and so were often lighter, with more air movement (C. Frost, personal observation). However, Chapter 3 showed that, overall, the edge did not significantly limit parasitoid movement in either direction. Observed parasitism rates matched expectations based on levels of shared parasitism and host abundances on the other side of the edge, regardless of which forest type was considered. Therefore, if the structural, abiotic, or other characteristics of the edge limited the movement of any parasitoid species, it did not do so overall, or for those species that contributed the most to predicted and realized apparent competition.

In a system with greater structural contrast, such as a grassland-forest edge, it is possible that productivity-driven natural enemy spillover would be mitigated by the sharper structural contrast, at least for some species (Ricketts, 2001). For the purpose of making conservation decisions, further work should look at how varying levels of structural contrast and productivity difference between habitats trade off to influence natural enemy spillover.

5.3 Plantation forest as a buffer between native forest and agricultural land

Although low structural contrast between habitats likely promotes spillover (Eycott *et al.*, 2012), it may lessen other edge effects (Didham and Lawton, 1999). Edge effects are often driven by abiotic changes at the edges of natural remnants, resulting from structural changes in the adjacent habitat, such as the clearing of tall trees (Harper *et al.*, 2005). For this reason, Brockerhoff *et al*. (2008) have proposed that plantation forest could be planted as a buffer around conservation forest, to separate the natural forest from cleared, high intensity agricultural land. They propose (not considering spillover) that this might be a viable technique for protecting natural forest from strong edge effects resulting from extreme structural contrast.

Considering this idea in light of my findings, the results from Chapter 2 showed that even the relatively small productivity difference between plantation and natural forest is sufficient to drive net spillover of natural enemies from plantation to native forest. This suggests that even a "buffer" of plantation forest could generate spillover edge effects in the native forest. However, apart from nutrient addition, spillover edge effects should only generate community change in the natural forest if they result in increased strength of direct or indirect interactions (Blitzer *et al.*, 2012). It is likely that in my study system, spillover of *Vespula* species caused strong direct and indirect effects in the natural forest (Barr *et al.*, 1996; Beggs and Rees, 1999; Wardle *et al.*, 2010). However, these predators may be a special case, in that they are non-native, highly invasive species, that are reportedly found at higher densities in New Zealand beech forests than anywhere else in the world (abundances in New Zealand plantation forests not having previously been measured; Beggs *et al.*, 2011). It is therefore possible that generalist predators in most systems would not impact native forest so extremely through spillover.

In fact, for the majority of the natural enemy species that I considered, i.e. the parasitoid guild, I detected no significant productivity-related asymmetry in direct effects (parasitism rates, Chapter 2) or indirect effects (apparent competition, Chapter 3) in the natural habitat, despite the asymmetric spillover of parasitoids (Chapter 2). It is possible

that I would have detected a significant asymmetry in apparent competitive effects if I had had a larger sample size of indirect interactions at training sites in Chapter 3, given that there was a non-significant trend toward this. However, as it stands, and with the exception of the effects of *Vespula* species, this work provides no robust evidence that the effects of plantation on native forest are any greater than the reciprocal effects of native forest on plantation forest. This is despite the fact that the plantation species, *Pinus radiata* is an exotic species, and that the plantation forest harbours high abundances of several other exotic plant species (see Chapter 2: *2.3.1*).

Therefore, while plantation forest as a buffer around native forest may not be beneficial in New Zealand, due to the increased *Vespula* wasp densities that this generates in native forest through spillover, it may be beneficial in other parts of the world (Brockerhoff *et al.*, 2008). Elsewhere, it may not result in strong functional change in the native forest, and may well accomplish the desired mitigation of the potentially more extreme edge effects that would result from juxtaposing native habitat and more intensively managed, structurally contrasting production land (Didham and Lawton, 1999; Cadenasso and Pickett, 2000). In the land sharing versus land sparing debate, Phalan *et al.* (2011) recently found that, overall, land sparing better achieved biodiversity conservation goals, while allowing for higher intensity agriculture. However, Chapter 2 suggests that higher-intensity production next to conservation land could exacerbate spillover of natural enemies from managed to natural systems. If the productivity difference was high enough, this might result in more significant direct and indirect effects on the native ecosystem than were detected here. Therefore, plantation buffer zones (Brockerhoff *et al.*, 2008) may be an imperfect compromise between the need for economic returns and the minimization of harm to adjacent natural habitats following spillover from high-productivity systems.

5.4 Apparent competition as a cross-habitat community structuring force, and implications for biological control

Although the impacts of cross-habitat spillover on natural systems have been a large focus of this thesis, I also found spillover from native to plantation forest (Chapter 2), and apparent competitive effects of herbivores in native forest on herbivores in

plantation forest (Chapter 3). These findings are interesting to consider in light of the potential for natural systems to provide natural pest control services to adjacent managed systems (Landis *et al.*, 2000). This is particularly the case given that, thus far, very few studies have approached biological control questions from a network perspective (Tylianakis and Binzer, 2013).

Host-parasitoid webs have become a popular focus in food-web research (e.g. Memmott *et al.*, 1994; Müller *et al.*, 1999; Lewis *et al.*, 2002; Valladares *et al.*, 2006; Barbosa *et al.*, 2007; Tylianakis *et al.*, 2007; Macfadyen *et al.*, 2009; de Sassi *et al.*, 2012), because of the relative ease with which trophic interactions can be quantified, relative to interactions involving generalist predators (van Veen *et al.*, 2006; but see Van Veen *et al.*, 2008). Classical biological control, as well as many integrated pest management strategies, involve parasitoids as control agents (Cruttwell McFadyen, 1998; Bianchi *et al.*, 2006), so there is potential for host-parasitoid network research to contribute to biological control programme development (Carvalheiro *et al.*, 2008; Macfadyen *et al.*, 2009; Tylianakis and Binzer, 2013). In particular, a network approach to biological control could contribute to understanding the indirect effects between species, which, when ignored, can often lead to unexpected results, such as non-target impacts (Carvalheiro *et al.*, 2008). In this thesis I have not focused on a pest system, and I did not include in the network chapters generalist predators, which are often important components of biological control (Symondson *et al.*, 2002; Snyder and Ives, 2003; Chailleux *et al.*, 2013). Nonetheless, Chapters 3 and 4 demonstrate concepts that could certainly be useful in understanding interactions, or predicting outcomes in pest insect systems.

Chapter 3 showed that the proportion of the parasitoids attacking a focal herbivore species that have recruited from another host species is significantly correlated to the level of apparent competition that the latter species will exert on the focal species. Thus, parasitism pressure can be significantly predicted for all species within a host-parasitoid assemblage, given quantitative information on shared parasitoids, and this is even the case across a habitat edge. In this way, the apparent competitive impact of non-pest herbivores within a system, including within non-cultivated field borders, could be

estimated, and introduction of a non-pest herbivore to act as an apparent competitor to a pest (Karban *et al.*, 1994) could be effectively planned.

Chapter 4 demonstrated that certain species traits can be used in place of quantitative information on parasitoid overlap to predict the strength and direction of apparent competition between herbivores. These traits could allow for relatively inexpensive estimation of the potential involvement in apparent competition of an introduced control agent with every other species within a host-parasitoid assemblage. Indirect effects have traditionally been a major obstacle to correctly predicting outcomes of control agent introductions (Cruttwell McFadyen, 1998), and apparent competition is believed to be one of the most important mechanisms through which indirect effects occur within host parasitoid assemblages (Morris *et al.*, 2004, 2005; van Veen *et al.*, 2006; Cronin, 2007; Tack *et al.*, 2011; van Nouhuys and Kraft, 2012). Therefore, these traits that correlate with involvement in apparent competition could be a very useful tool for incorporating important indirect effects in predictions about outcomes of biological control introductions.

5.5 Sampling quantitative interactions in a biological community

A caveat to the work presented here, in particular Chapters 3 and 4, is that lepidopteran larval rearing success was less than 50%. This would not be problematic if the successes were an unbiased sample of interactions. However, it is difficult to know whether this is the case, and any bias is impossible to quantify. For example, first instar larvae were the most likely to die during rearing, so my rearing would have been biased against detecting interactions mediated by parasitoids that preferentially attack first instars, such as some Campopleginae species (Gauld, 1984). It is unknown how parasitoids attacking hosts in early instars may contribute differently to apparent competition within the community than parasitoids attacking in later instars. However, given the generally high mortality rates of juvenile insects in nature, which may also include parasitized and unparasitized individuals, it is even possible that my high rearing mortality was quite representative of what happens in forests.

The problem of low rearing success plagues quantitative food-web studies (e.g., Memmott *et al.*, 1994; Lewis *et al.*, 2002; Valladares *et al.*, 2006). In earlier studies, this

was often acknowledged, along with other potential shortcomings of quantitative food webs as representations of reality (Memmott *et al.*, 1994; Müller *et al.*, 1999; Lewis *et al.*, 2002), but a solution is difficult to find. When rearing large numbers of different species, for which natural history is not individually known, and for which rearing protocols have not been individually developed, it is practically impossible to achieve perfect rearing success.

A further caveat to such a study involving parasitoid species, which are mostly undescribed, and for which the natural history can only be guessed from higher taxon generalizations, is that it can be difficult to distinguish parasitism events from hyperparasitism events. In this work, I excluded reared *Euceros coxalis* and *Mesochorus* species from the bipartite food webs, since these are known hyperparasitoids, or within predominantly hyperparasitoid subfamilies, respectively (Gauld, 1984). However, there may have been other unknown hyperparasitoids that I failed to exclude. As well, I had no way to distinguish parasitism from hyperparasitism for facultative hyperparasitoids.

At this point, further development of molecular identification techniques seems like a promising solution to these problems in the future. Yet currently, although powerful DNA sequencing techniques are available, and more affordable than ever (Gut, 2013), it would still be difficult to isolate and amplify parasitoid DNA from within a host for all the hosts collected during large-community sampling. It would be even more difficult to identify a parasitoid and a hyperparasitoid within the same host, without having a species-level primer library available. This is because, if both parasitoid and hyperparasitoid DNA were picked up by the same general primer, a nonsensical chimera of parasitoid and hyperparasitoid DNA could be assembled from short-read sequences.

Until molecular identification tools are refined or exhaustive natural history information is compiled, we are left with imperfect detection of quantitative feeding interactions in host-parasitoid systems. However, while quantitative food web data could be further enhanced, the resolution offered here allows us a first intriguing glimpse into some of the fundamental properties of trophic interactions in nature. The finding in Chapter 3 that the quantitative food-web data could successfully predict parasitism rates at nearby locations lends strong support to this idea.

5.6 Conclusions and future directions

The overarching objective of this thesis was to investigate whether herbivore biomass drives spillover of predators between habitats, and whether that spillover of predators changes species interactions in the recipient habitat. The answer to this question could inform landscape planning to achieve conservation of remnant natural areas amidst production land. I found asymmetrical spillover, as predicted based on productivity differences between managed and natural habitats (Rand *et al.*, 2006). In the case of generalist *Vespula* species, I also found experimentally that levels of spillover from plantation to native forest depended on herbivore abundance in the plantation forest. Spillover-driven increases in the density of these predators likely has far-reaching impacts on the native forest (Beggs *et al.*, 2011).

I found little evidence of asymmetrical apparent competition between herbivores in the native and plantation forests, based on quantitative host-parasitoid interactions pooled across two seasons. I did, however, find that hosts across the habitat edge were coupled in apparent competition, such that if there were, for example, a pest outbreak in the plantation forest, this would have cascading apparent competitive effects on herbivore populations across the edge.

Surprisingly, I found no evidence that a significant herbivore density reduction in the plantation forest had any effect on parasitoid direct interactions in native forest. This could have been because my manipulation of the herbivore abundance in plantation forest may have been biased against killing herbivores that hosted parasitoids. However, it could also have been because the native forest trophic interaction network was resistant to perturbation. It could be that herbivore reduction of a similar magnitude in a certain habitat would have had a greater impact on trophic interactions in an adjacent habitat, if the adjacent habitat had had a less-complex food web structure than that within a diverse native forest (Ives and Carpenter, 2007). Areas of conservation concern within production landscapes are not always forests, and may be simpler communities that are more vulnerable to spillover-related change, such as grasslands or wetlands. Future work should look at how structural contrast between habitats (as discussed in section *5.2*) and food-web structure of a recipient habitat mitigate the impacts of spillover on trophic interactions in the recipient habitat. This should be examined over a range of productivity

gradients between habitats. Only by studying all of these potentially interacting factors together will we be able to make general predictions about the effect of production land adjacent to conservation land on trophic interactions in both ecosystems.

The second major objective of this thesis was to understand how generally apparent competition (or apparent mutualism) occurs as predicted by parasitoid overlap, both within and across habitats. The finding in Chapter 3 that across the entire host-parasitoid assemblage from both habitats, parasitism rates could be predicted based on quantitative information on parasitoid overlap, initial attack rates, and the change in host abundances, is very exciting. It suggests that, as predicted by Müller *et al.* (1999), parasitoid overlap does significantly predict realized apparent competition, as opposed to apparent mutualism (Tack *et al.*, 2011), and does so for all species pairs within a community. Historically, indirect effects have been difficult to incorporate explicitly into dynamic models (Laska and Wootton, 1998; O'Gorman *et al.*, 2010) or to predict in complex communities (Yodzis, 1988; Montoya *et al.*, 2009). The ability to predict apparent competition in entire host-parasitoid assemblages is a great step towards understanding what may be the most important type of indirect effect to structure these assemblages (Morris *et al.*, 2005; van Veen *et al.*, 2006). Furthermore, the discovery of species traits that correlate with degree of involvement in apparent competition promises great utility for this work in biological control.

However, apparent competition does not only occur between hosts that share parasitoids. Many published examples of apparent competition involve prey species that share a generalist predator (e.g., Menge, 1995; Oliver *et al.*, 2009; Long *et al.*, 2012), and apparent competitive motifs occur commonly in non-parasitoid food webs (Bascompte and Melian, 2005). Therefore, it is likely that apparent competition in non-parasitoid food webs could also occur regularly, and be predictable based on shared predator attack rates. However, because the dynamics of generalist predator populations are less dependent on individual prey dynamics than is the case for parasitoids (Beddington *et al.*, 1978), predator-prey interactions are often more flexible and transient than parasitoid-host interactions (Rooney *et al.*, 2006; Scotti *et al.*, 2007). Given this, apparent competition is not likely to be as important in structuring food webs as it is for host-parasitoid webs

(Morris *et al.*, 2005), and methods of prediction cannot simply be extrapolated from host-parasitoid work (Scotti *et al.*, 2007).

As discussed in section *5.5*, quantitative food webs are very difficult to compile for non-parasitoid food webs, which would seem to make predictions of their indirect effects unfeasible currently. However, a relatively simple agricultural, pest-based system might be a tractable place to start. At least a set of the strongest interactions within such a system might already be roughly quantifiable through a combination of stable isotope analysis (Hyodo *et al.*, 2010), gut-content analysis (King *et al.*, 2008), and herbivore 'bait' observation experiments (Karban *et al.*, 2013).

Within host-parasitoid webs, further work should look at the timescale over which community-wide apparent competitive effects are the strongest. Temporal population fluxes of herbivore pests can be extreme in crop systems (Rand *et al.*, 2006). This renders understanding the timing of apparent competitive effects key to predicting their impact on biological control of herbivores. Within forests, it would be interesting to look at whether vertical distance represents more of a barrier to apparent competitive effects than does a horizontal habitat boundary. This may be the case, given that Paniagua *et al.* (2009) found very different food-web structure in the canopy versus the understorey of tropical forests, and less parasitoid overlap within the canopy than within the understorey. As well, previous work has shown that canopy-understorey interactions can be vertically unidirectional, because gravity assists movement downward and restricts movement upwards (Pringle and Fox-Dobbs, 2008).

Global change drivers, such as land-use change, threaten entire ecosystems, and thus we will have to understand ecosystem-level processes in order to predict and mitigate undesired change, such as spillover edge effects (Rand *et al.*, 2006). Within ecosystems, communities of interacting species perform vital functions (Chapin *et al.*, 2000). Disentangling the mechanisms by which indirect effects cascade through trophic links within communities will be key to predicting community-level responses to disturbance of all kinds (Montoya *et al.*, 2009), and an important step towards protecting those crucial links in complex interacting communities (McCann, 2007; Tscharntke and Tylianakis, 2010).

Bibliography.

Abrams, P.A., 1983. Arguments in favor of higher-order interactions. American Naturalist 121, 887-891.

Abrams, P.A., 2004. Trait-initiated indirect effects due to changes in consumption rates in simple food webs. Ecology 85, 1029-1038.

Abrams, P.A., Holt, R.D., Roth, J.D., 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. Ecology 79, 201-212.

Alhmedi, A., Haubruge, E., D'Hoedt, S., Francis, F., 2011. Quantitative food webs of herbivore and related beneficial community in non-crop and crop habitats. Biological Control 58, 103-112.

Angelstam, P., 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47, 365-373.

Araújo, E.D., Costa, M., Chaud-Netto, J., Fowler, H.G., 2004. Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. Brazilian Journal of Biology 64, 563-568.

Armsworth, P.R., Chan, K.M.A., Daily, G.C., Ehrlich, P.R., Kremen, C., Ricketts, T.H., Sanjayan, M.A., 2007. Ecosystem-service science and the way forward for conservation. Conservation Biology 21, 1383-1384.

Austin, A.D., and Dangerfield, P.C., 1992. Synopsis of Australasian Microgastrinae (Hymenoptera: Braconidae), with a key to genera and description of new taxa. Invertebrate Taxonomy 6, 1-76.

Baayen, R.H., 2010. languageR: Data sets and functions with "Analyzing Linguistic Data: A practical introduction to statistics". R package version 1.0. http://CRAN.R-project.org/package=lme4.

Banasek-Richter, C., Cattin, M.F., Bersier, L.F., 2004. Sampling effects and the robustness of quantitative and qualitative food-web descriptors. Journal of Theoretical Biology 226, 23-32.

Barbosa, P., Caldas, A., Godfray, H.C.J., 2007. Comparative food web structure of larval macrolepidoptera and their parasitoids on two riparian tree species. Ecological Research 22, 756-766.

Barr, K., Moller, H., Christmas, E., Lyver, P., Beggs, J., 1996. Impacts of introduced common wasps (Vespula vulgaris) on experimentally placed mealworms in a New Zealand beech forest. Oecologia 105, 266-270.

Barratt, B.I.P., Howarth, F.G., Withers, T.M., Kean, J.M., Ridley, G.S., 2010. Progress in risk assessment for classical biological control. Biological Control 52, 245-254.

Bascompte, J., Melian, C.J., 2005. Simple trophic modules for complex food webs. Ecology 86, 2868-2873.

Bastolla, U., Fortuna, M.A., Pascual-Garcia, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458, 1018-U1091.

Bates, D., Maechler, M., and Bolker, B., 2011. lme4: Linear mixed-effects models using S4 classes.

Bauce, E., Carisey, N., Dupont, A., Van Frankenhuyzen, K., 2004. Bacillus thuringiensis subsp kurstaki aerial spray prescriptions for balsam fir stand protection against spruce budworm (Lepidoptera : Tortricidae). Journal of Economic Entomology 97, 1624-1634.

Beddington, J.R., Free, C.A., Lawton, J.H., 1978. Characteristics of successful natural enemies in models of biological control of insect pests. Nature 273, 513-519.

Beggs, J.R., Brockerhoff, E.G., Corley, J.C., Kenis, M., Masciocchi, M., Muller, F., Rome, Q., Villemant, C., 2011. Ecological effects and management of invasive alien Vespidae. Biocontrol 56, 505-526.

Beggs, J.R., Rees, J.S., 1999. Restructuring of Lepidoptera communities by introduced *Vespula* wasps in a New Zealand beech forest. Oecologia 119, 565-571.

Begon, M., Harper, J.L., Townsend, C.R., 1986. Ecology: Individuals, Populations and Communities. Sinauer Associates, Sunderland, Mass., U.S.A.

Berry, J.A., 1997. *Meteorus pulchricornis* (Wesmael) (Hymenoptera: Braconidae: Euphorinae), a new record for New Zealand. New Zealand Entomologist 20, 45-48.

Berry, J.A., Walker, G.P., 2004. Meteorus pulchricornis (Wesmael) (Hymenoptera: Braconidae: Euphorinae): an exotic polyphagous parasitoid in New Zealand. New Zealand Journal of Zoology 31, 33-44.

Bianchi, F., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B-Biological Sciences 273, 1715-1727.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agriculture, Ecosystems & Environment 146, 34-43.

Blitzer, E.J., Welter, S.C., 2011. Emergence asynchrony between herbivores leads to apparent competition in the field. Ecology 92, 2020-2026.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127-135.

Bonsall, M.B., Hassell, M.P., 1997. Apparent competition structures ecological assemblages. Nature 388, 371-373.

Brassil, C.E., Abrams, P.A., 2004. The prevalence of asymmetrical indirect effects in two-host-one-parasitoid systems. Theoretical Population Biology 66, 71-82.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17, 925-951.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771-1789.

Brown, W.L., Wilson, E.O., 1956. Character displacement. Systematic Zoology 5, 49-64.

Cadenasso, M.L., Pickett, S.T.A., 2000. Linking forest edge structure to edge function: mediation of herbivore damage. Journal of Ecology 88, 31-44.

Cadenasso, M.L., Pickett, S.T.A., 2001. Effect of edge structure on the flux of species into forest interiors. Conservation Biology 15, 91-97.

Callicott, J.B., Crowder, L.B., Mumford, K., 1999. Current normative concepts in conservation. Conservation Biology 13, 22-35.

Campbell, R.E., Harding, J.S., Ewers, R.M., Thorpe, S., Didham, R.K., 2011. Production land use alters edge response functions in remnant forest invertebrate communities. Ecological Applications 21, 3147-3161.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. Bioscience 35, 634-639.

Carvalheiro, L.G., Buckley, Y.M., Memmott, J., 2010. Diet breadth influences how the impact of invasive plants is propagated through food webs. Ecology 91, 1063-1074.

Carvalheiro, L.G., Buckley, Y.M., Ventim, R., Fowler, S.V., Memmott, J., 2008. Apparent competition can compromise the safety of highly specific biocontrol agents. Ecology Letters 11, 690-700.

Chailleux, A., Bearez, P., Pizzol, J., Amiens-Desneux, E., Ramirez-Romero, R., Desneux, N., 2013. Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest *Tuta absoluta*. Journal of Pest Science 86, 533-541.

Chalak, M., Hemerik, L., van der Werf, W., Ruijs, A., van Ierland, E.C., 2010. On the risk of extinction of a wild plant species through spillover of a biological control agent: Analysis of an ecosystem compartment model. Ecological Modelling 221, 1934-1943.

Chaneton, E.J., Bonsall, M.B., 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. Oikos 88, 380-394.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. Nature 405, 234-242.

Closs, G.P., Balcombe, S.R., Shirley, M.J., 1999. Generalist predators, interaction strength and food-web stability. Advances in Ecological Research, Vol 28 28, 93-126.

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T.C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D.D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C.H., Seidel, D., Steffan-Dewenter, I., Stenchly, K., Vidal, S., Weist, M., Wielgoss, A.C., Tscharntke, T., 2011. Combining high biodiversity with high yields in tropical agroforests. Proceedings of the National Academy of Sciences of the United States of America 108, 8311-8316.

Costanza, R., d'Arge, R., Groot, R.d., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Belt, M.v.d., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.

Crawley, M., 2007. The R Book. John Wiley and Sons, West Sussex, England.

Cronin, J.T., 2007. Shared parasitoids in a metacommunity: Indirect interactions inhibit herbivore membership in local communities. Ecology 88, 2977-2990.

Cruttwell McFadyen, R.E., 1998. Biological control of weeds. Annual Review of Entomology 43, 369-393.

D'Adamo, P., Lozada, M., 2008. Foraging behaviour in *Vespula germanica* wasps re-locating a food source. New Zealand Journal of Zoology 35, 9-17.

Daily, G.C., Soderqvist, T., Aniyar, S., Arrow, K., Dasgupta, P., Ehrlich, P.R., Folke, C., Jansson, A., Jansson, B.O., Kautsky, N., Levin, S., Lubchenco, J., Maler, K.G., Simpson, D., Starrett, D., Tilman, D., Walker, B., 2000. Ecology - The value of nature and the nature of value. Science 289, 395-396.

Dawson, J., Lucas, R., 2000. Nature Guide to the New Zealand Forest. Godwit, Auckland, N.Z.

Didham, R.K., Denmead, L.H., Deakin, E.L., 2012. Riches to rags: the ecological consequences of land-use intensification in New Zealand. In: Lindenmayer, D.B., Cunningham, S.A., Young, A.D. (Eds.), Land Use Intensification: Effects on Agriculture, Biodiversity and Ecological Processes. CSIRO, Canberra, Australia, pp. 73-83.

Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented forests: A functional approach. Trends in Ecology and Evolution 11, 255-260.

Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31, 17-30.

Dobson, A., Lodge, D., Alder, J., Cumming, G.S., Keymer, J., McGlade, J., Mooney, H., Rusak, J.A., Sala, O., Wolters, V., Wall, D., Winfree, R., Xenopoulos, M.A., 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology 87, 1915-1924.

Dormann, C.F., Gruber, B., Fruend, J., 2008. Introducing the bipartite package: Analysing Ecological Networks. R News 8, 8-11.

Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic and Applied Ecology 4, 129-138.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters 5, 558-567.

Eagle, A., 2006. Eagle's Complete Trees and Shrubs of New Zealand. Te Papa Press, Wellington.

Edgar, R.C., 2004. MUSCLE: A multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics 5, 1-19.

Elliott, G.P., Wilson, P.R., Taylor, R.H., Beggs, J.R., 2010. Declines in common, widespread native birds in a mature temperate forest. Biological Conservation 143, 2119-2126.

Emmerson, M.C., Raffaelli, D., 2004. Predator-prey body size, interaction strength and the stability of a real food web. Journal of Animal Ecology 73, 399-409.

Enfjäll, K., Leimar, O., 2005. Density-dependent dispersal in the Glanville fritillary, Melitaea cinxia. Oikos 108, 465-472.

Erisman, J.W., Galloway, J.N., Seitzinger, S., Bleeker, A., Dise, N.B., Petrescu, A.M.R., Leach, A.M., de Vries, W., 2013. Consequences of human modification of the global nitrogen cycle. Philosophical Transactions of the Royal Society B-Biological Sciences 368.

Ernest, S.K.M., Enquist, B.J., Brown, J.H., Charnov, E.L., Gillooly, J.F., Savage, V., White, E.P., Smith, F.A., Hadly, E.A., Haskell, J.P., Lyons, S.K., Maurer, B.A., Niklas, K.J., Tiffney, B., 2003. Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecology Letters 6, 990-995.

Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., Pullin, A.S., 2012. A meta-analysis on the impact of different matrix structures on species movement rates. Landscape Ecology 27, 1263-1278.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. Science 281, 237-240.

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16, 265-280.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570-574.

Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics 19, 207-233.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhoffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyorgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters 14, 1062-1072.

Gauld, I.D., 1984. An introduction to the Ichneumonidae of Australia. British Museum of Natural History, London, U.K.

Gladbach, D.J., Holzschuh, A., Scherber, C., Thies, C., Dormann, C.F., Tscharntke, T., 2011. Crop-noncrop spillover: arable fields affect trophic interactions on wild plants in surrounding habitats. Oecologia 166, 433-441.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food Security: The Challenge of Feeding 9 Billion People. Science 327, 812-818.

Gols, R., Harvey, J.A., 2009. Plant-mediated effects in the Brassicaceae on the performance and behaviour of parasitoids. Phytochemistry Reviews 8, 187-206.

Gomez, J.M., Perfectti, F., Jordano, P., 2011. The Functional Consequences of Mutualistic Network Architecture. Plos One 6.

Goudard, A., Loreau, M., 2008. Nontrophic interactions, biodiversity, and ecosystem functioning: An interaction web model. American Naturalist 171, 91-106.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. Science 307, 550-555.

Gut, I.G., 2013. New sequencing technologies. Clinical and Translational Oncology 15, 879-881.

Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.A., 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19, 768-782.

Harris, R.J., 1991. Diet of the wasps *Vespula vulgaris* and *Vespula germanica* in honeydew beech forest of the South Island, New-Zealand. New Zealand Journal of Zoology 18, 159-169.

Hawkins, B.A., 1994. Pattern and Process in Host-Parasitoid Interactions. Cambridge University Press, Cambridge.

Henri, D.C., Van Veen, F.J.F., 2011. Body Size, Life History and the Structure of Host-Parasitoid Networks. In: Belgrano, A., Reiss, J. (Eds.), Advances in Ecological Research, Vol 45: The Role of Body Size in Multispecies Systems, pp. 135-180.

Hirao, T., Murakami, M., 2008. Quantitative food webs of lepidopteran leafminers and their parasitoids in a Japanese deciduous forest. Ecological Research 23, 159-168.

Hoare, R.J.B., Rhode, B.E., Emmerson, A.W., 2011 (and updates). Larger moths of New Zealand: Image gallery and online guide. http://www.landcareresearch.co.nz/resources/identification/animals/large-moths

Holt, R.D., 1977. Predation, apparent competition, and structure of prey communities. Theoretical Population Biology 12, 197-229.

Holt, R.D., 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124, 377-406.

Holt, R.D., Hochberg, M.E., 2001. Indirect interactions, community modules and biological control: a theoretical perspective. In: Wajnberg, E., Scott, J.K., Quimby, P.C. (Eds.), Evaluating Indirect Ecological Effects of Biological Control. CAB International, Wallingford, pp. 13-37.

Holt, R.D., Kotler, B.P., 1987. Short-term apparent competition. American Naturalist 130, 412-430.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75, 3-35.

Hrcek, J., Miller, S.E., Whitfield, J.B., Shima, H., Novotny, V., 2013. Parasitism rate, parasitoid community composition and host specificity on exposed and semi-concealed caterpillars from a tropical rainforest. Oecologia 173, 521-532.

Huddleston, T., 1986. The braconid genus *Meteorus* in New Zealand (Insecta: Hymenoptera). Journal of Natural History 20, 255-265.

Hudson, G.V., 1928. The Butterflies and Moths of New Zealand. Ferguson & Osborn Ltd., Wellington.

Hudson, G.V., 1939. A Supplement to the Butterflies and Moths of New Zealand. Ferguson & Osborn Ltd., Wellington.

Hughes, R.N., Croy, M.I., 1993. An experimental-analsysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia*-spinachia. Journal of Animal Ecology 62, 341-352.

Huxel, G.R., McCann, K., Polis, G.A., 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. Ecological Research 17, 419-432.

Hyodo, F., Matsumoto, T., Takematsu, Y., Kamoi, T., Fukuda, D., Nakagawa, M., Itioka, T., 2010. The structure of a food web in a tropical rain forest in Malaysia based on carbon and nitrogen stable isotope ratios. Journal of Tropical Ecology 26, 205-214.

Ings, T.C., Montoya, J.M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H., Woodward, G., 2009. Ecological networks - beyond food webs. Journal of Animal Ecology 78, 253-269.

IPCC, I.P.o.C.C., 2007. Climate Change 2007: The physical science basis. IPCC WGI Fourth Assessment Report, Geneva, p. 21.

Ishii, Y., Shimada, M., 2012. Learning predator promotes coexistence of prey species in host-parasitoid systems. Proceedings of the National Academy of Sciences of the United States of America 109, 5116-5120.

Ito, H.C., Kondo, N.I., 2012. Biological pest control by investing crops in pests. Population Ecology 54, 557-571.

Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. Science 317, 58-62.

Jackson, H.B., Baum, K.A., Robert, T., Cronin, J.T., 2009. Habitat-specific movement and edge-mediated behavior of the saproxylic insect odontotaenius disjunctus (coleoptera: Passalidae). Environmental Entomology 38, 1411-1422.

Jefferies, R.L., 2000. Allochthonous inputs: integrating population changes and food-web dynamics. Trends in Ecology & Evolution 15, 19-22.

Jetz, W., Carbone, C., Fulford, J., Brown, J.H., 2004. The scaling of animal space use. Science 306, 266-268.

Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. Journal of Applied Ecology 49, 706-714.

Jonsson, T., Cohen, J.E., Carpenter, S.R., 2005. Food webs, body size, and species abundance in ecological community description. Advances in Ecological Research, Vol 36, pp. 1-84.

Kaartinen, R., Roslin, T., 2013. Apparent competition leaves no detectable imprint on patterns of community composition: observations from a natural experiment. Ecological Entomology 38, 522-530.

Kaiser, C.N., Hansen, D.M., Mueller, C.B., 2008. Exotic pest insects: another perspective on coffee and conservation. Oryx 42, 143-146.

Karban, R., Hougeneitzmann, D., Englishloeb, G., 1994. Predator-mediated apparent competition between 2 herbivores that feed on grapevines. Oecologia 97, 508-511.

Karban, R., Mata, T.M., Grof-Tisza, P., Crutsinger, G., Holyoak, M.A., 2013. Non-trophic effects of litter reduce ant predation and determine caterpillar survival and distribution. Oikos 122, 1362-1370.

Kareiva, P., Watts, S., McDonald, R., Boucher, T., 2007. Domesticated nature: Shaping landscapes and ecosystems for human welfare. Science 316, 1866-1869.

King, R.A., Read, D.S., Traugott, M., Symondson, W.O.C., 2008. Molecular analysis of predation: A review of best practice for DNA-based approaches. Molecular Ecology 17, 947-963.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B-Biological Sciences 274, 303-313.

Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A., Holt, R.D., 2005. Trophic cascades across ecosystems. Nature 437, 880-883.

Kuefler, D., Hudgens, B., Haddad, N.M., Morris, W.F., Thurgate, N., 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology 91, 944-950.

Lahti, D.C., 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99, 365-374.

Lahti, D.C., 2009. Why we have been unable to generalize about bird nest predation. Animal Conservation 12, 279-281.

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45, 175-201.

Laska, M.S., Wootton, J.T., 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79, 461-476.

Laurance, W.F., Didham, R.K., Power, M.E., 2001. Ecological boundaries: a search for synthesis. Trends in Ecology and Evolution 16, 70-71.

Lavandero, B., Tylianakis, J.M., 2013. Genotype matching in a parasitoid-host genotypic food web: an approach for measuring effects of environmental change. Molecular Ecology 22, 229-238.

Leathwick, D.M., 1997. Growth and development of queen colonies of Vespula germanica and V. vulgaris. New Zealand Journal of Zoology 24, 17-23.

Lewis, O.T., Memmott, J., Lasalle, J., Lyal, C.H.C., Whitefoord, C., Godfray, H.C.J., 2002. Structure of a diverse tropical forest insect-parasitoid community. Journal of Animal Ecology 71, 855-873.

Long, W.C., Gamelin, E.F., Johnson, E.G., Hines, A.H., 2012. Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system. Marine Ecology Progress Series 456, 139-148.

Lutz, W., Samir, K.C., 2010. Dimensions of global population projections: what do we know about future population trends and structures? Philosophical Transactions of the Royal Society B-Biological Sciences 365, 2779-2791.

M.E.A., 2005. Millenium Ecosystem Assessment: Ecosystems and Human Well-Being: Scenarios. Island Press, Washington D.C., USA.

Macfadyen, S., Gibson, R., Polaszek, A., Morris, R.J., Craze, P.G., Planque, R., Symondson, W.O.C., Memmott, J., 2009. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? Ecology Letters 12, 229-238.

Macfadyen, S., Muller, W., 2013. Edges in Agricultural Landscapes: Species Interactions and Movement of Natural Enemies. Plos One 8, e59659.

Magurran, A.E., 2009. Measuring Biological Diversity. John Wiley & Sons, Chichester.

Maskell, L.C., Crowe, A., Dunbar, M.J., Emmett, B., Henrys, P., Keith, A.M., Norton, L.R., Scholefield, P., Clark, D.B., Simpson, I.C., Smart, S.M., 2013. Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity. Journal of Applied Ecology 50, 561-571.

McCann, K., 2007. Protecting biostructure. Nature 446, 29.

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228-233.

McCann, K.S., Rasmussen, J.B., Umbanhowar, J., 2005. The dynamics of spatially coupled food webs. Ecology Letters 8, 513-523.

McKone, M.J., McLauchlan, K.K., Lebrun, E.G., McCall, A.C., 2001. An edge effect caused by adult corn-rootworm beetles on sunflowers in tallgrass prairie remnants. Conservation Biology 15, 1315-1324.

Memmott, J., 2009. Food webs: a ladder for picking strawberries or a practical tool for practical problems? Philosophical Transactions of the Royal Society B-Biological Sciences 364, 1693-1699.

Memmott, J., Godfray, H.C.J., Gauld, I.D., 1994. The Structure of a Tropical Host Parasitoid Community. Journal of Animal Ecology 63, 521-540.

Menge, B.A., 1995. Indirect Effects in Marine Rocky Intertidal Interaction Webs - Patterns and Importance. Ecological Monographs 65, 21-74.

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloom, E.W., Torchin, M.E., Vazquez, D.P., 2006. Biotic interactions and plant invasions. Ecology Letters 9, 726-740.

Montoya, J.M., Rodriguez, M.A., Hawkins, B.A., 2003. Food web complexity and higher-level ecosystem services. Ecology Letters 6, 587-593.

Montoya, J.M., Woodward, G., Emmerson, M.C., Sole, R.V., 2009. Press perturbations and indirect effects in real food webs. Ecology 90, 2426-2433.

Morris, R.J., Lewis, O.T., Godfray, H.C.J., 2004. Experimental evidence for apparent competition in a tropical forest food web. Nature 428, 310-313.

Morris, R.J., Lewis, O.T., Godfray, H.C.J., 2005. Apparent competition and insect community structure: towards a spatial perspective. Annales Zoologici Fennici 42, 449-462.

Muhire, B., Martin, D.P., Brown, J.K., Navas-Castillo, J., Moriones, E., Zerbini, F.M., Rivera-Bustamante, R., Malathi, V.G., Briddon, R.W., Varsani, A., 2013. A genome-wide pairwise-identity-based proposal for the classification of viruses in the genus Mastrevirus (family Geminiviridae). Archives of Virology 158, 1411-1424.

Müller, C.B., Adriaanse, I.C.T., Belshaw, R., Godfray, H.C.J., 1999. The structure of an aphid-parasitoid community. Journal of Animal Ecology 68, 346-370.

Müller, C.B., Godfray, H.C.J., 1997. Apparent competition between two aphid species. Journal of Animal Ecology 66, 57-64.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10, 58-62.

Nakamura, T., Kimura, M.T., 2009. Weak parasitoid-mediated apparent competition between two Phyllonorycter (Lepidoptera: Gracillariidae) leaf miner species on a deciduous oak Quercus dentata. Entomological Science 12, 227-231.

Norris, R.F., Kogan, M., 2000. Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems. Weed Science 48, 94-158.

O'Connor, N.E., Emmerson, M.C., Crowe, T.P., Donohue, I., 2013. Distinguishing between direct and indirect effects of predators in complex ecosystems. Journal of Animal Ecology 82, 438-448.

O'Gorman, E.J., Jacob, U., Jonsson, T., Emmerson, M.C., 2010. Interaction strength, food web topology and the relative importance of species in food webs. Journal of Animal Ecology 79, 682-692.

Oksanen, T., 1990. Exploitation ecosystems in heterogeneous habitat complexes. Evolutionary Ecology 4, 220-234.

Oksanen, T., Oksanen, L., Gyllenburg, M., 1992. Exploitation ecosystems in heterogeneous habitat complexes II: impact of small-scale heterogeneity on predator-prey dynamics. Evolutionary Ecology 6, 383-398.

Oliver, M., Luque-Larena, J.J., Lambin, X., 2009. Do rabbits eat voles? Apparent competition, habitat heterogeneity and large-scale coexistence under mink predation. Ecology Letters 12, 1201-1209.

Orrock, J.L., Holt, R.D., Baskett, M.L., 2010. Refuge-mediated apparent competition in plant-consumer interactions. Ecology Letters 13, 11-20.

Orrock, J.L., Witter, M.S., 2010. Multiple drivers of apparent competition reduce re-establishment of a native plant in invaded habitats. Oikos 119, 101-108.

Östman, Ö., Ives, A.R., 2003. Scale-dependent indirect interactions between two prey species through a shared predator. Oikos 102, 505-514.

Ovington, J.D., Lawrence, D.B., Heitkamp, D., 1963. Plant biomass and productivity of prairie, savanna, oakwood, and maize field ecosystems in central Minnesota. Ecology 44, 52-63.

Paniagua, M.R., Medianero, E., Lewis, O.T., 2009. Structure and vertical stratification of plant galler-parasitoid food webs in two tropical forests. Ecological Entomology 34, 310-320.

Paynter, Q., Martin, N., Berry, J., Hona, S., Peterson, P., Gourlay, A.H., Wilson-Davey, J., Smith, L., Winks, C., Fowler, S.V., 2008. Non-target impacts of Phytomyza vitalbae a biological control agent of the European weed *Clematis vitalba* in New Zealand. Biological Control 44, 248-258.

Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F., Araujo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guenette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for Global Biodiversity in the 21st Century. Science 330, 1496-1501.

Pfennig, D.W., Rice, A.M., Martin, R.A., 2006. Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. Ecology 87, 769-779.

Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. Science 333, 1289-1291.

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidised food webs. Annual Review of Ecology and Systematics 28, 289-316.

Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. The American Naturalist 147, 813-846.

Pringle, R.M., Fox-Dobbs, K., 2008. Coupling of canopy and understory food webs by ground-dwelling predators. Ecology Letters 11, 1328-1337.

Rand, T.A., Louda, S.A., 2006. Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. Conservation Biology 20, 1720-1729.

Rand, T.A., Tscharntke, T., 2007. Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. Oikos 116, 1353-1362.

Rand, T.A., Tylianakis, J.M., Tscharntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecology Letters 9, 603-614.

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Recart, W., Ackerman, J.D., Cuevas, A.A., 2013. There goes the neighborhood: apparent competition between invasive and native orchids mediated by a specialist florivorous weevil. Biological Invasions 15, 283-293.

Reimchen, T.E., Fox, C.H., 2013. Fine-scale spatiotemporal influences of salmon on growth and nitrogen signatures of Sitka spruce tree rings. BMC Ecology 13.

Ricketts, T.H., 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist 158, 87-99.

Ries, L., Debinski, D.M., 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. Journal of Animal Ecology 70, 840-852.

Ries, L., Fletcher, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annual Review of Ecology Evolution and Systematics 35, 491-522.

Romo, C.M., Tylianakis, J.M., 2013. Elevated Temperature and Drought Interact to Reduce Parasitoid Effectiveness in Suppressing Hosts. Plos One 8, e58136

Rooney, N., McCann, K., Gellner, G., Moore, J.C., 2006. Structural asymmetry and the stability of diverse food webs. Nature 442, 265-269.

Rosenberg, A.A., 2003. Managing to the margins: the overexploitation of fisheries. Frontiers in Ecology and the Environment 1, 102-106.

Rott, A.S., Godfray, H.C.J., 2000. The structure of a leafminer-parasitoid community. Journal of Animal Ecology 69, 274-289.

Sackett, T.E., Buddle, C.M., Vincentb, C., 2009. Dynamics of spider colonization of apple orchards from adjacent deciduous forest. Agriculture Ecosystems & Environment 129, 144-148.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770-1774.

Sale, M.G., Arnould, J.P.Y., 2012. Inflated population density of island antechinus: a case of allochthonous marine inputs leading to increased food availability? Australian Journal of Zoology 60, 343-351.

Sanders, D., Sutter, L., van Veen, F.J.F., 2013. The loss of indirect interactions leads to cascading extinctions of carnivores. Ecology Letters 16, 664-669.

Sarfraz, M., Dosdall, L.M., Keddie, B.A., 2008. Host plant genotype of the herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) affects the performance of its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). Biological Control 44, 42-51.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18-32.

Schmitt, R.J., 1987. Indirect interactions between prey – apparent competition, predator aggregation, and habitat segregation. Ecology 68, 1887-1897.

Schnitzler, F.-R., Ward, D.F., 2013. Key to Ichneumonidae in New Zealand. http://www.landcareresearch.co.nz/resources/identification/animals/ichneumonidae

Schonrogge, K., Crawley, M.J., 2000. Quantitative webs as a means of assessing the impact of alien insects. Journal of Animal Ecology 69, 841-868.

Schultz, C.B., Franco, A.M.A., Crone, E.E., 2012. Response of butterflies to structural and resource boundaries. Journal of Animal Ecology 81, 724-734.

Scotti, M., Podani, J., Jordan, F., 2007. Weighting, scale dependence and indirect effects in ecological networks: A comparative study. Ecological Complexity 4, 148-159.

Sears, A.L.W., Holt, R.D., Polis, G.A., 2004. Feast or famine in food webs: the effects of pulsed productivity. In: Polis, G.A., Power, M.E., Huxel, G.R. (Eds.), Food Webs At The Landscape Level. The University of Chicago Press, Chicago.

Settle, W.H., Wilson, L.T., 1990. Invasion by the Variegated Leafhopper and Biotic Interactions - Parasitism, Competition, and Apparent Competition. Ecology 71, 1461-1470.

Sheehan, W., Shelton, A.M., 1989. Parasitoid response to concentration of herbivore food plants – finding and leaving plants. Ecology 70, 993-998.

Simberloff, D., 2012. Risks of biological control for conservation purposes. Biocontrol 57, 263-276.

Simberloff, D., Stiling, P., 1996. How risky is biological control? Ecology 77, 1965-1974.

Smith, M.A., Wood, D.M., Janzen, D.H., Hallwachs, W., Hebert, P.D.N., 2007. DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera, Tachinidae) are not all generalists. Proceedings of the National Academy of Sciences of the United States of America 104, 4967-4972.

Smith, M.A., Woodley, N.E., Janzen, D.H., Hallwachs, W., Hebert, P.D.N., 2006. DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera : Tachinidae). Proceedings of the National Academy of Sciences of the United States of America 103, 3657-3662.

Snyder, W.E., Ives, A.R., 2003. Interactions between specialist and generalist natural enemies: Parasitoids, predators, and pea aphid biocontrol. Ecology 84, 91-107.

Southwood, T.R.E., 1988. Tactics, strategies and templets. Oikos 52, 3-18.

Squires, S.E., Hermanutz, L., Dixon, P.L., 2009. Agricultural insect pest compromises survival of two endemic Braya (Brassicaceae). Biological Conservation 142, 203-211.

Steinmetz, I., Schmolz, E., 2004. Influence of illuminance and forager experience on use of orientation cues in social wasps (Vespinae). Journal of Insect Behavior 17, 599-612.

Stevens, V.M., Leboulengé, É., Wesselingh, R.A., Baguette, M., 2006. Quantifying functional connectivity: Experimental assessment of boundary permeability for the natterjack toad (*Bufo calamita*). Oecologia 150, 161-171.

Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47, 561-594.

Tack, A.J.M., Gripenberg, S., Roslin, T., 2011. Can we predict indirect interactions from quantitative food webs? - an experimental approach. Journal of Animal Ecology 80, 108-118.

Tallis, H., Kareiva, P., Marvier, M., Chang, A., 2008. An ecosystem services framework to support both practical conservation and economic development. Proceedings of the National Academy of Sciences of the United States of America 105, 9457-9464.

Tate, K.R., Giltrap, D.J., Claydon, J.J., Newsome, P.F., Atkinson, I.A.E., Taylor, M.D., Lee, R., 1997. Organic carbon stocks in New Zealand's terrestrial ecosystems. Journal of the Royal Society of New Zealand 27, 315-335.

Thebault, E., Fontaine, C., 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. Science 329, 853-856.

Thomas, C.F.G., Parkinson, L., Marshall, E.J.P., 1998. Isolating the components of activity-density for the carabid beetle Pterostichus melanarius in farmland. Oecologia 116, 103-112.

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., Tylianakis, J.M., 2012. Food webs: reconciling the structure and function of biodiversity. Trends in Ecology & Evolution 27, 689-697.

Tillman, P.G., Powell, J.E., 1991. Developmental time in relation to temperature for *Microplitis croceipes, M. demolitor, Cotesia kazak* (Hymenoptera: Braconidae), and *Hyposoter didymator* (Hymenoptera: Ichneumonidae), endoparasites of the tobacco budworm (Lepidoptera: Noctuidae). Environmental Entomology 20, 61-64.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292, 281-284.

Trotter, C., Tate, K., Scott, N., Townsend, J., Wilde, H., Lambie, S., Marden, M., Pinkney, T., 2005. Afforestation/reforestation of New Zealand marginal pasture lands by indigenous shrublands: the potential for Kyoto forest sinks. Annals of Forest Science 62, 865-871.

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012a. Global food security, biodiversity conservation and the future of agricultural intensification. Biological Conservation 151, 53-59.

Tscharntke, T., Rand, T.A., Bianchi, F., 2005. The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. Annales Zoologici Fennici 42, 421-432.

Tscharntke, T., Tylianakis, J., 2010. Conserving complexity: Global change and community-scale interactions. Biological Conservation 143, 2249-2250.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Frund, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012b. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87, 661-685.

Turchin, P., 1989. Population consequences of aggregative movement. Journal of Animal Ecology 58, 75-100.

Tylianakis, J.M., Binzer, A., 2013. Effects of global environmental changes on parasitoid-host food webs and biological control. Biological Control, In Press.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11, 1351-1363.

Tylianakis, J.M., Laliberte, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. Biological Conservation 143, 2270-2279.

Valladares, G.R., Salvo, A., Godfray, H.C.J., 2001. Quantitative food webs of dipteran leafminers and their parasitoids in Argentina. Ecological Research 16, 925-939.

van Achterberg, C., Berndt, L., Brockerhoff, E., and Berry, J., 2004. A new species of genus *Aleiodes* Wesmael from New Zealand (Hymenoptera: Braconidae: Rogadinae). Zoologische Mededelingen 78, 301-311.

Van Maanen, R., Messelink, G.J., Van Holstein-Saj, R., Sabelis, M.W., Janssen, A., 2012. Prey temporarily escape from predation in the presence of a second prey species. Ecological Entomology 37, 529-535.

van Nouhuys, S., Kraft, T.S., 2012. Indirect interaction between butterfly species mediated by a shared pupal parasitoid. Population Ecology 54, 251-260.

van Veen, F.J.F., Brandon, C.E., Godfray, H.C.J., 2009. A positive trait-mediated indirect effect involving the natural enemies of competing herbivores. Oecologia 160, 195-205.

van Veen, F.J.F., Morris, R.J., Godfray, H.C.J., 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. Annual Review of Entomology 51, 187-208.

Van Veen, F.J.F., Mueller, C.B., Pell, J.K., Godfray, H.C.J., 2008. Food web structure of three guilds of natural enemies: predators, parasitoids and pathogens of aphids. Journal of Animal Ecology 77, 191-200.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, W., Schlesinger, H., Tilman, D., 1997. Human alteration of the global nitrogen cycle- sources and consequences. Ecological Applications 7, 737-750.

Wahl, D.B.a.S., M.J., 1993. Superfamily Ichneumonoidea. In: Goulet, H.a.H., J.T. (Ed.), Hymenoptera of the world: an identification guide to families. Agriculture Canada, Ottawa, Canada.

Walker, A.K., 1996. A new species of *Choeras* (Braconidae: Microgastrinae) widespread in New Zealand. New Zealand Entomologist 19, 43-48.

Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kuhn, I., Zobel, M., Bacher, S., Botta-Dukat, Z., Bugmann, H., Czucz, B., Dauber, J., Hickler, T., Jarosik, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vila, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Trends in Ecology & Evolution 24, 686-693.

Wardhaugh, C.W., Didham, R.K., 2006. Preliminary evidence suggests that beech scale insect honeydew has a negative effect on terrestrial litter decomposition rates in *Nothofagus* forests of New Zealand. New Zealand Journal of Ecology 30, 279-284.

Wardle, D.A., Karl, B.J., Beggs, J.R., Yeates, G.W., Williamson, W.M., Bonner, K.I., 2010. Determining the impact of scale insect honeydew, and invasive wasps and rodents, on the decomposer subsystem in a New Zealand beech forest. Biological Invasions 12, 2619-2638.

Williamson, M.H., 1957. Elementary theory of interspecific competition. Nature 180, 422-425.

Wilson, E.O., 1984. Biophilia. Harvard University Press, Cambridge, MA, USA.

Woodward, G., Ebenman, B., Ernmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. Trends in Ecology & Evolution 20, 402-409.

Wootton, J.T., 1993. Indirect effects and habitat use in an intertidal community – interaction chains and interaction modifications. American Naturalist 141, 71-89.

Wootton, J.T., 2002. Indirect effects in complex ecosystems: recent progress and future challenges. Journal of Sea Research 48, 157-172.

Wright, M.G., Hoffmann, M.P., Kuhar, T.P., Gardner, J., Pitcher, S.A., 2005. Evaluating risks of biological control introductions: A probabilistic risk-assessment approach. Biological Control 35, 338-347.

Yodzis, P., 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69, 508-515.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York, U.S.A.

Zuur, A.F., Saveliev, A.A., and Ieno, E.N, 2012. Zero inflated models and generalized linear mixed models with R. Highland Statistics Ltd, Newburgh, U.K.

Appendix 1

A.1.1 Tables of species sampled

Table S1.1 Plant species from which lepidopteran larvae were collected. In the 'Dataset' column, 1 refers to the 'training sites' of Ch. 3 and the 'two-season dataset' of Ch. 4, whereas 2 refers to the 'validation sites' of Ch. 3 and the 'one-season dataset' of Ch. 4. 'Both' means that lepidopteran larvae were collected from that species at both sets of sites.

Family	Species	Dataset
Araliaceae	*Pseudopanax arboreus* (L.f.) Allan	Both
	Pseudopanax crassifolius (Sol. ex A.Cunn.) C.Koch	Both
	Raukaua anomalus (Hook.f.) A.D.Mitch., Frodin et Heads	Both
	Schefflera digitata J.R.Forst. et G.Forst.	Both
Araucariaceae	*Agathis australis* (D.Don) Lindl.	2
Aspleniaceae	*Asplenium bulbiferum* G. Forst.*	Both
	Asplenium flaccidum G.Forst.	2
	Asplenium oblongifolium Colenso	1
	Asplenium polyodon G.Forst.	Both
Asteliaceae	*Astelia* Banks & Sol. ex R.Br. sp.	2
Asteraceae	*Brachyglottis repanda* J.R.Forst. & G.Forst.	1
	Helichrysum dimorphum Cockayne	2
	Helichrysum lanceolatum (Buchanan) Kirk	Both
	Olearia rani var. *colorata* (Colenso) Kirk	Both
	Olearia avicenniifolia (Raoul) Hook.f.	1
	Senecio L. sp.	1
Berberidaceae	*Berberis* L. sp.	1
Blechnaceae	*Blechnum discolor* (G.Forst.) Keyserl.**	Both
	Blechnum fluviatile (R.Br.) Salomon	2
	Blechnum minus (R.Br.) Ettingsh.	1
	Blechnum novae-zelandiae T.C.Chambers et P.A.Farrant*	2
	Blechnum procerum (G.Forst.) Sw.**	2
Caprifoliaceae	*Leycesteria formosa* Wall.	Both
Coriariaceae	*Coriaria arborea* R.Linds. var. *arborea*	Both
Cunoniaceae	*Weinmannia racemosa* L.f.	Both
Cyatheaceae	*Cyathea colensoi* (Hook.f.) Domin	Both
	Cyathea dealbata (G.Forst.) Sw.*	Both
	Cyathea medullaris (G.Forst.) Sw.	1
	Cyathea smithii Hook. f.*	Both
Cyperaceae	*Gahnia* J.R. & G. Forst*	2
	Uncinia Pers. sp.*	2
Dennstaedtiaceae	*Histiopteris incisa* (Thunb.) J. Sm.	Both
	Pteridium esculentum (G. Forst.) Cockayne	Both
Dicksoniaceae	*Dicksonia fibrosa* Colenso*	2
	Dicksonia L'Hér. sp.	Both

	Dicksonia squarrosa (G.Forst.) Swartz[*]	2
Dryopteridaceae	*Polystichum neozelandicum* Fée subsp. *neozelandicum*[*]	2
	Polystichum vestitum (G. Forst.) C. Presl	Both
Elaeocarpaceae	*Aristotelia serrata* (J.R.Forst. et G.Forst.) W.R.B.Oliv.	Both
	Elaeocarpus dentatus (J.R.Forst. et G.Forst.) Vahl var. *dentatus*	Both
	Elaeocarpus hookerianus Raoul	1
Ericaceae	*Erica lusitanica* Rudolphi	Both
	Gaultheria antipoda G.Forst.	Both
	Leptecophylla juniperina (J.R.Forst. et G.Forst.) C.M.Weiller subsp. *juniperina*[*]	Both
	Leucopogon fasciculatus (G.Forst.) A.Rich.	Both
Fabaceae	*Carmichaelia* sp. R.Br.	2
	Chamaecytisus palmensis (H.Christ) F.A.Bisby & K.W.Nicholls	1
	Ulex europaeus L.	Both
Gramineae	*Cortaderia richardii* (Endl.) Zotov.	1
Griseliniaceae	*Griselinia littoralis* Raoul	Both
	Griselinia lucida G.Forst.	1
Lauraceae	*Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex Kirk	Both
Lycopodiaceae	*Lycopodium volubile* G.Forst.	1
Marattiaceae	*Marattia salicina* Sm.	1
Monimiaceae	*Hedycarya arborea* J.R.Forst. et G.Forst.	Both
Myrtaceae	*Kunzea ericoides* (A.Rich) Joy Thomps. var. *ericoides*	Both
	Leptospermum scoparium J.R.Forst. et G.Forst. var. *scoparium*	Both
	Lophomyrtus bullata Burret	Both
	Lophomyrtus obcordata (Raoul) Burret	1
	Metrosideros carminea W.R.B.Oliv.	2
	Metrosideros diffusa (G.Forst.) Sm.	Both
	Metrosideros fulgens Sol. ex Gaertn.	Both
	Metrosideros perforata (J.R.Forst. et G.Forst.) A.Rich.[****]	2
	Neomyrtus pedunculata (Hook.f.) Allan	Both
Nothofagaceae	*Fuscospora fusca* (Hook.f.) Heenan et Smissen	Both
	Fuscospora solandri (Hook.f.) Heenan et Smissen	Both
	Fuscospora truncata (Colenso) Heenan et Smissen	Both
	Lophozonia menziesii (Hook.f.) Heenan et Smissen	Both
Oleaceae	*Nestegis montana* (Hook.f.) L.A.S.Johnson[*]	Both
Onagraceae	*Fuchsia excorticata* (J.R.Forst. et G.Forst.) L.f.	Both
Osmundaceae	*Leptopteris hymenophylloides* (A.Rich.) C.Presl	Both
Paracryphiaceae	*Quintinia serrata* A.Cunn.	1
Passifloraceae	*Passiflora tetrandra* Banks ex DC.	1
Pennantiaceae	*Pennantia corymbosa* J.R.Forst. et G.Forst.	Both
Pinaceae	*Pinus radiata* D. Don	Both
	Pinus sylvestris L.	1
	Pseudotsuga menziesii (Mirb.) Franco	1
Pittosporaceae	*Pittosporum divaricatum* Cockayne	2
	Pittosporum eugenioides A.Cunn.	Both
	Pittosporum rigidum Hook.f., 1852	1
	Pittosporum tenuifolium Sol. ex Gaertn.[*]	Both
Plantaginaceae	*Digitalis purpurea* L.	Both
Poaceae	*Austroderia richardii* (Endl.) N.P.Barker et H.P.Linder	2
	Microlaena avenacea (Raoul.) Hook.f.[*]	2
Podocarpaceae	*Dacrycarpus dacrydioides* (A.Rich.) de Laub.[**]	2

	Dacrydium cupressinum Lamb.	1
	Podocarpus cunninghamii Colenso	Both
	Podocarpus totara G.Benn. ex D.Don var. *totara*	1
	Prumnopitys ferruginea (D.Don) Laubenf.	1
	Prumnopitys taxifolia (D.Don) de Laub.	1
Polygonaceae	*Muehlenbeckia australis* (G.Forst.) Meisn.**	2
Polypodiaceae	*Microsorum pustulatum* (G. Forst.) Copel. subsp. *pustulatum* **	Both
	Microsorum scandens (G.Forst.) Tindale	1
Primulaceae	*Myrsine australis* (A.Rich.) Allan	Both
Ranunculaceae	*Clematis forsteri* J.F.Gmel.***	2
Ripogonaceae	*Ripogonum scandens* J.R.Forst. et G.Forst.	Both
Rosaceae	*Crataegus monogyna* Jacq.	2
	Rubus australis G.Forst.	2
	Rubus cissoides A.Cunn.	Both
	Rubus fruticosus L. agg.	Both
Rousseaceae	*Carpodetus serratus* J.R.Forst. et G.Forst.	Both
Rubiaceae	*Coprosma areolata* Cheeseman	1
	Coprosma ciliata Hook.f.	2
	Coprosma colensoi Hook.f.	Both
	Coprosma dumosa (Cheeseman) G.T.Jane	2
	Coprosma foestidissima J.R.Forst. et G.Forst.	Both
	Coprosma grandifolia Hook.f.	Both
	Coprosma aff *intertexta* G. Simpson	1
	Coprosma linariifolia Hook.f.	Both
	Coprosma lucida J.R.Forst. et G.Forst.*	Both
	Coprosma microcarpa Hook.f.	Both
	Coprosma propinqua A.Cunn. var. *propinqua*	Both
	Coprosma propinqua x *robusta* Raoul*	Both
	Coprosma rhamnoides A.Cunn.	Both
	Coprosma robusta Raoul*	Both
	Coprosma rotundifolia A.Cunn.**	Both
Sapindaceae	*Alectryon excelsus* Gaertn. subsp. *excelsus***	Both
Thelypteridaceae	*Pneumatopteris pennigera* (G. Forst.) Holttum**	2
Thymelaeaceae	*Pimelea gnidia* (J.R.Forst. et G.Forst.) Willd.***	2
Urticaceae	*Urtica ferox* G.Forst.	2
Violaceae	*Melicytus ramiflorus* J.R.Forst. et G.Forst.	Both
Winteraceae	*Pseudowintera axillaris* (J.R.Forst. et G.Forst.) Dandy	Both
	Pseudowintera colorata (Raoul) Dandy*	Both
Xanthorrhoeaceae	*Dianella nigra* Colenso	1
	Phormium tenax J.R.Forst. et G.Forst.	Both

* Voucher specimens deposited in the University of Canterbury Herbarium, with the number of stars representing the number of specimens of that species deposited. Vouchers of the other plant species have been deposited as Guadalupe Peralta's thesis collection in the University of Canterbury Herbarium.

Table S1.2 Lepidoptera species sampled. Starred (*****) morphospecies represent cases in which two or more congeneric species were lumped into a single morphospecies because larvae of the lumped species were indistinguishable. Taxonomist John Dugdale assisted with larval and adult identifications. In the 'Dataset' column, 1 refers to the 'training sites' of Ch. 3 and the 'two-season dataset' of Ch. 4, whereas 2 refers to the 'validation sites' of Ch. 3 and the 'one-season dataset' of Ch. 4. 'Both' means that lepidopteran larvae of that species were collected in both datasets.

Family	Species	Dataset
Arctiidae	*Nyctemera annulata* (Boisduval, 1832)	1
Carposinidae	*Heterocrossa gonosemana* Meyrick, 1882	1
	Heterocrossa Meyrick, 1882 sp. 'indet A'	Both
	Paramorpha marginata (Philpott, 1931)	1
Crambidae	*Deana hybreasalis* (Walker, 1859)	Both
	Musotima nitidalis (Walker, 1866)	1
Gelechiidae	*Thiotricha* Meyrick, 1886 sp. *****	1
	Thiotricha lindsayi Philpott, 1927	1
Geometridae	*Austrocidaria* Dugdale, 1971 sp. *****	Both
	Chalastra pellurgata Walker, 1862	Both
	Chloroclystis Hubner, [1825] sp. *****	Both
	Cleora scriptaria (Walker, 1860)	Both
	Declana feredayi Butler, 1877	Both
	Declana floccosa Walker, 1858	Both
	Declana hermione Hudson, 1898	1
	Declana junctilinea (Walker, 1865)	Both
	Declana leptomera (Walker, 1858)	Both
	Declana niveata Butler, 1879	1
	Elvia glaucata Walker, 1862	1
	Gellonia Meyrick, 1884 sp. *****	Both
	Helastia Guenée, 1868 sp. *****	1
	Hydriomena deltoidata (Walker, 1862)	1
	Ischalis gallaria (Walker, 1860)	Both
	Ischalis nelsonaria (Felder & Rogenhofer, 1875)	2
	Ischalis variabilis (Warren, 1895)	Both
	Pasiphila sandycias (Meyrick, 1905)	Both
	Poecilasthena Warren, 1894 sp. *****	Both
	Pseudocoremia ampla (Hudsonb, 1923)	1
	Pseudocoremia fascialata (Philpott, 1903)	1
	Pseudocoremia fenerata (Felder & Rogenhofer, 1875)	Both
	Pseudocoremia fluminea (Philpott, 1926)	1
	Pseudocoremia leucelaea (Meyrick, 1909)	Both
	Pseudocoremia lupinata (Felder & Rogenhofer, 1875)	Both
	Pseudocoremia productata (Walker, 1862)	Both
	Pseudocoremia Butler, 1877 sp. *****	Both
	Sarisa muriferata (Walker, 1863)	1
	Sestra Walker, 1862 sp. *****	Both
	Tatosoma agrionata Walker, 1862	2
	Tatosoma lestevata (Walker, 1862)	1
	Tatosoma tipulata (Walker, 1862)	Both
	Xyridacma sp. *****	Both

Gracillariidae	*Caloptilia linearis* (Butler, 1877)	Both
	Caloptilia selenitis (Meyrick, 1909)	1
Noctuidae	*Austramathes purpurea* (Butler, 1879)	Both
	Andesia pessota (Meyrick, 1887)	1
	Chrysodeixis eriosoma (Doubleday, 1843)	1
	Diarsia intermixta (Guenée, 1852)	2
	Feredayia graminosa (Walker, 1857)	Both
	Graphania chlorodonta (Hampson, 1911)	2
	Graphania insignis (Walker, 1865)	1
	Graphania mutans (Walker, 1857)	1
	Graphania phricias Meyrick 1887	2
	Graphania plena (Walker, 1865)	Both
	Graphania prionistis (Meyrick, 1887)	2
	Graphania ustistriga (Walker, 1857)	Both
	Meterana dotata (Walker, 1857)	Both
	Meterana meyricci Hampson, 1911	2
	Meterana ochthistis Meyrick, 1887	2
	Meterana pascoi (Howes, 1912)	1
	Meterana tartarea (Butler, 1877)	2
	Meterana vitiosa (Butler, 1877)	Both
	Physetica prionistis Meyrick, 1887	1
	Physetica sequens Howes, 1912	1
	Rhapsa scotosialis Walker, 1866	Both
Nolidae	*Celama parvitis* Howes, 1917	Both
Oecophoridae	*Eutorna phaulocosma* Meyrick, 1906	1
	Gymnobathra Meyrick, 1883 sp.	1
	Nymphostola galactina (Felder & Rogenhofer, 1875)	Both
	Phaeosaces Meyrick, 1886 sp. *****	Both
	Proteodes profunda Meyrick, 1905	Both
Plutellidae	*Orthenches* Meyrick, 1886 sp.	Both
Psychidae	*Grypotheca pertinax* Dugdale, 1987	1
	Lepidoscia heliochares (Meyrick, 1893)	2
	Liothula omnivore Fereday, 1878	Both
	Psychidae 4.spots	2
	Psychidae other	2
	Psychidae sp 2	2
	Vanicela disjunctella Walker	2
Stathmopodidae	*Stathmopoda* Herrich-Schaffer, 1853 sp. 'chocolate'	Both
	Erechthias Meyrick, 1880 cf. chionodira	2
Tineidae	*Erechthias externella* (Walker, 1864)	1
	Opogona comptella Walker, 1864	2
	Sagephora phortegella Meyrick, 1888	1
Tortricidae	*Apoctena* Dugdale, 1990 sp. *****	Both
	Catamacta gavisana (Walker, 1863)	Both
	Cnephasia jactatana (Walker, 1863)	Both
	Ctenopseustis Meyrick, 1885 sp. *****	Both
	Dipterina imbriferana Meyrick, 1881	Both
	Ecclitica torogramma (Meyrick, 1897)	Both
	Epalxiphora axenana Meyrick, 1881	1
	Epichorista emphanes (Meyrick, 1901)	Both

	Epichorista hemiona (Meyrick, 1882)	1
	Epichorista Meyrick, 1909 sl.allogama	2
	Epiphyas postvittana (Walker, 1863)	1
	Harmologa amplexana (Zeller, 1875)	1
	Holocola dolopaea Meyrick, 1905	2
	Holocola emplasta Meyrick, 1901	1
	Holocola parthenia Meyrick, 1888	Both
	Holocola zopherana Meyrick, 1881	1
	Leucotenes coprosmae (Dugdale, 1988)	Both
	Planotortrix excessana (Walker, 1863)	Both
	Planotortrix Dugdale, 1966 octo + notophaea *****	Both
	Pyrgotis plagiatana (Walker, 1863)	Both
	Pyrgotis pyramidias Meyrick, 1901	Both
	Strepsicrates Meyrick, 1881 sp.	1
Yponomeutidae	*Kessleria copidota* (Meyrick, 1889)	1

Table S1.3 Parasitoid species reared. In the 'Dataset' column, 1 refers to the 'training sites' of Ch. 3 and the 'two-season dataset' of Ch. 4, whereas 2 refers to the 'validation sites' of Ch. 3 and the 'one-season dataset' of Ch. 4. 'Both' means that that parasitoid species was reared in both datasets.

Order	Family	Species	Dataset
Diptera	Tachinidae	*Calcager dubium* Malloch, 1938	Both
		Calcageria incidens Curran, 1927	Both
		Genotrichia minor Malloch, 1938	1
		Genotrichia Malloch, 1938 sp. 1	Both
		Montanarturia dimorpha (Malloch, 1938)	1
		Pales atrox (Hutton, 1901)	1
		Pales casta (Hutton, 1904)	1
		Pales clathrata (Nowicki, 1875)	Both
		Pales feredayi (Hutton, 1901)	Both
		Pales funesta (Hutton, 1901)	Both
		Pales marginata (Hutton, 1901)	Both
		Pales Robineau-Desvoidy, 1830 sp. 1	2
		Plagiomyia longipes Malloch, 1938	1
		Trigonospila brevifacies (Hardy, 1934)	Both
		Uclesiella Malloch, 1938 sp.	1
Hymenoptera	Bethylidae	*Eupsenella* Westwood, 1874 sp. 1	2
		Sierola Cameron, 1881 sp. 1	2
	Braconidae	*Aleiodes* Wesmael, 1838 sp.	Both
		Choeras Mason, 1981 sp.	Both
		Cotesia Cameron, 1891 sp.	1
		Dolichogenidea Viereck, 1911 'darklegs' sp. 4	Both
		Dolichogenidea Viereck, 1911 'lightly punct'	Both
		Glyptapanteles Ashmead, 1904 'dark'	Both
		Glyptapanteles Ashmead, 1904 sp. 2	Both
		Glyptapanteles Ashmead, 1904 sp. 3	Both
		Glyptapanteles Ashmead, 1904 sp. 4	Both
		Glyptapanteles Ashmead, 1904 sp. 5	Both
		Glyptapanteles Ashmead, 1904 sp. 6	1
		Glyptapanteles Ashmead, 1904 sp. 8	1
		Meteorus cinctellus (Spinolla, 1808)	Both
		Meteorus cobbus Huddleston, 1986	1
		Meteorus pulchricornis (Wesmael, 1835)	Both
	Eulophidae	*Sympiesis* Forster, 1856 sp.	Both
		Zealachertus Boucek, 1978 sp.	1
		Zealachertus tortriciphaga Berry, 1999	1
	Ichneumonidae	*Aucklandella* Cameron, 1909 sp.	1
		Campoletis Forster, 1868 sp. 1	Both
		Campoletis Forster, 1868 sp. 4	1
		Campoletis Forster, 1868 sp. 5	1
		Campoletis Forster, 1868 sp. 9	1
		Campoplex Gravenhorst, 1829 sp. 1	1
		Campoplex Gravenhorst, 1829 sp. 13	Both
		Campoplex Gravenhorst, 1829 sp. 16	2
		Campoplex Gravenhorst, 1829 sp. 2	1

	Campoplex Gravenhorst, 1829 sp. 3	Both
	Campoplex Gravenhorst, 1829 sp. 4	1
	Campoplex Gravenhorst, 1829 sp. 9	Both
	Carria Schmiedeknecht, 1924 sp.	Both
	Casinaria Holmgren, 1858 sp. 3	Both
	Diadegma Forster, 1868 'brown '	Both
	Diadegma Forster, 1868 'gold setae'	Both
	Diadegma Forster, 1868 sp. 1	Both
	Diadegma Forster, 1868 sp. 3	1
	Diadegma Forster, 1868 sp. 4	2
	Genus nov. Hearthead	1
	Ophion Fabricius, 1798 sp.	Both
	Phytodietus Gravenhorst, 1829 sp.	1
	Sciron Fitton, 1984 sp.	Both
Torymidae	Torymidae.sp1	2

A.1.2 Tables of parasitoid voucher specimens deposited

Since most of the parasitoids sampled were from undescribed species, I deposited all parasitoid specimens in one of three collections: 1) The Museum of Wellington Te Papa Tongarewa, Wellington; 2) the New Zealand Arthropod Collection, Landcare Research, Auckland; and 3) the University of Canterbury, Christchurch (care of Prof. Jason Tylianakis).

Table S1.4 Reared parasitoid voucher specimens from the Ch. 3 'validation' sites. Specimens of species in the family Braconidae were deposited in the Museum of Wellington Te Papa Tongarewa, and all other specimens were deposited in the New Zealand Arthropod Collection, Landcare Research, Auckland. (Underlined specimens have been deposited instead in the University of Canterbury, care of Prof. Jason Tylianakis.) Bolded highlighted specimens were DNA-barcoded, and sequences have been uploaded onto BOLD Systems (www.boldsystems.org), under the project name 'University of Canterbury Ichneumonidae'. (For species taxonomic authorities, see Table S1.3.)

a) Order Hymenoptera

Family	Subfamily	Species	Specimens
Braconidae	Meteorinae	*Meteorus cinctellus*	**M-6297**, M-8417, M-9149, M-9992
		Meteorus pulchricornis	M-3765, M-3880, M-3970, M-4085, M-5976, M-6034, M-6182, M-6240, M-7086, M-7292, M-7392, M-7598, M-7623, M-7828, M-10585
	Microgastrinae	*Choeras* sp.	M-207, M-269, **M-273**, **M-352**, **M-354**, M-364, M-441, M-629, M-752, **M-805**, M-1654, M-2640, M-3016, **M-3018**, M-3262, M-3307, **M-3354**, **M-3380**, M-3455, M-3466, M-3718, **M-4778**
		Dolichogenidea darklegs sp.4	M-1248, M-1979, M-3735, M-4171, M-5740, M-5922, M-6318, M-6323, M-6332, M-6335, M-6339, M-6374, M-6410, M-6448, M-6541, M-6943, M-6996, M-7083, M-7089, M-7118, M-7163, M-7262, M-7778, M-7944, M-8180, M-8184, M-8186, **M-8187**, M-8388, **M-8529**, M-8559, M-8563, M-8569, M-8573, M-8604, M-8608, M-8636, M-8796, M-8955, M-9172, M-9426, M-9836, M-10196, M-10217, M-10681, M-10715
		Dolichogenidea lightly punct.	**M-2419**, M-2792, **M-3167**, M-3575, **M-3849**, M-3973, **M-4038**, **M-4635**, M-5168, M-5228, M-5557, M-5608, M-5633, M-5639, M-5743, **M-5765**, M-5872, **M-6127**, M-6128, M-6195, M-6209, **M-6320**, M-6328, M-6341, **M-6371**, **M-6416**, M-6421, **M-6493**, M-6521, M-6648, M-6854, **M-6906**, **M-7011**, M-7065, M-7080, **M-7091**, **M-7096**, M-7098, **M-7109**, M-7150, M-7289, **M-7295**, M-7308, **M-7480**, M-7714, **M-7718**, M-7874, M-7970, **M-8147**, M-8254, M-8300, M-8360, **M-8393**, M-8427, M-8467, **M-8489**, M-8493, M-8498, **M-8501**, M-8502, **M-8524**, M-8556, **M-8617**, M-8620, **M-8627**, **M-8679**, **M-8720**, M-8771, M-8921, M-9021, M-9299, M-9314, M-9328, **M-9429**, M-9476, M-9660, M-9677, M-9699, M-9710, **M-9747**, **M-9808**, M-9829, M-9955, M-9971, M-9974, M-9976, M-9991, M-9993, M-10119, **M-10452**, M-10505, M-10559, **M-10613**, M-10657, M-10691, **M-10694**, **M-10696**, M-10737
		Dolichogenidea sp.	M-9803
		Glyptapanteles sp.	M-7668
		Glyptapanteles sp. 2	**M-3183**, **M-3804**, **M-3908**, M-4693, **M-5660**, M-5823, M-7839, M-8600, M-9593, M-9655
		Glyptapanteles sp. 3	M-2201, M-2693, M-3428, M-3431, M-3729, M-3795, M-3926, M-4380, M-4864, M-7185, M-7720
		Glyptapanteles sp. 4	M-4250, M-4516, M-7389, M-7400, M-9196
		Glyptapanteles sp. 5	**M-2577**, M-3609, **M-4229**, **M-4514**, **M-5196**, **M-5612**, **M-6163**, M-6396, **M-6449**, **M-6542**, **M-6794**, M-7265, **M-7324**, M-7340, **M-7593**, **M-8216**, M-8398, **M-8655**, **M-8656**, M-8658, **M-8872**, **M-9019**, **M-9043**, M-9110, **M-9684**, **M-10420**, **M-10438**, M-10526, M-10629, M-10654
		Glyptapatales dark	**M-6530**
		Aleiodes sp.	M-2498, M-3219, **M-4313**, M-4593, M-4768, M-4974, M-5122, M-5138, **M-5170**, M-5250, M-5706, M-6547, M-6898, M-6923, M-6929, M-7031, M-7254, **M-7279**, M-8318, M-8557, **M-9120**, M-9939, M-10014
Eulophidae	Eulophinae	*Sympiesis* sp.	M-2622, M-4517, M-6264A, M-6264B, M-9221A
Ichneumonidae	Campopleginae	*Campoletis* sp. 1	M-4716, M-6494, M-8457, M-9637
		Campoletis sp. 4	**M-391**, **M-9965**
		Campoplex sp.	M-3758, **M-5891**, M-8347, M-8465

		Campoplex sp. 13	**M-97**, M-159, M-1310, M-1341, M-1759, M-2371, M-2390, M-2536, M-2549, M-3278, M-3302, M-4323, M-4699, **M-9228**, M-9229, M-10466 M-10700, M-10704
		Campoplex sp. 16	M-2120
		Campoplex sp. 3	M-885, M-1062, **M-4116**, M-6236, M-6267, **M-7059**, M-7824, M-7904, M-8460, M-8471, **M-8488**, **M-10396**
		Campoplex sp. 9	M-5918, M-5970, M-7020, M-7257, M-8256, M-8402, M-8404, M-8459, **M-8466**, **M-8478**, M-8517, M-8521, M-8525, M-9146, M-9678, M-9743, M-9757, M-9979, M-9995, M-10626
		Casinaria sp. 3	M-1431, **M-1465**, M-3860, **M-4451B**
		Diadegma brown	**M-490**, M-3008, M-3721, M-3897, M-5094, M-5956
		Diadegma gold setae	M-2055, M-2578, **M-2626**, M-3230, M-4501, M-4532
		Diadegma sp. 1	M-1934, M-3856, M-3885, M-5626, M-5748, M-6052, **M-6072**, M-6252, M-6271, M-6361, M-6756, M-7028, M-7048, M-7250, M-7387, M-7582B, M-7601, M-7635, M-7753, M-7800, M-7865, M-8190, M-8246, M-8436, M-8464, M-8475, M-8492, M-8618, M-8708, M-9240, M-9366, M-9478, M-9679, M-9761, M-9790, M-9802, M-9872, M-10200, M-10537, M-10591, M-10692
		Diadegma sp. 4	M-6183
	Eucerotinae	*Euceros coxalis*	M-4681; 1/6 M-4681; 2/6
	Ichneumoninae	*Eutanyacra* sp. 1	M-8364
	Mesochorinae	*Mesochorus* shiny brown	M-6667, M-7069, M-8305, M-8399, M-8483, M-8777, M-9174, M-10005, M-10460
		Mesochorus sp. 1	M-4320; 1 of 12 M-4320; 2 of 12 M-4320; 3 of 12 **M-4726**, M-4747, M-4802, M-6487, M-8231, M-8371, M-9108
		Mesochorus sp. 4	**M-6776**
		Mesochorus yellow face	**M-4611**
		Carria sp.	M-3868, M-5571, M-8392
		Sciron sp.	M-4056B, M-4098, M-4128, M-4145, M-4156, M-4174, M-4183, M-4185, M-4189, M-4207, M-4221, M-4236
	Ophioninae	*Ophion* sp.	M-168, M-3216, **M-4022**, M-4625
Platygastridae	?	Platygastridae sp. 1	M-2354, M-10337
Torymidae	?	Torymidae sp. 1	M-2350

b) Order Diptera

Family	**Subfamily**	**Species**	**Specimens**
Tachinidae	Exoristinae	*Pales clathrata*	M-1168
		Pales feredayi	M-8565
		Pales funesta	M-2575, M-3905, M-3916, M-3979, M-5301, M-6601, M-7182, M-8009, M-8049, M-8055, M-8414, M-8962
		Pales marginata	M-3436, M-7738, M-8395, M-9226
		Pales sp. 1	M-8001
		Trigonospila brevifacies	M-9367
	Tachininae	*Calcager dubium*	M-3931
	?	*Calcageria incidens*	M-4314, M-4594, M-5391, M-5621, M-9527
		Genotrichia sp. 1	M-4192

Table S1.5 Trapped Braconidae morphospecies, and the specimens deposited as vouchers in the Museum of Wellington Te Papa Tongarewa, Wellington, New Zealand. (Underlined highlighted specimens have been deposited instead at the University of Canterbury, Christchurch, care of Prof. Jason Tylianakis.)

Subfamily	Morphospecies	Specimens
Agathidinae	Agathidinae sp. 1	7EHLOW2P.1/02/11.b2, 4ECLOW4P.1/02/11.b6, 16EHHIGH3N.1/03/11.b1, 16EHHIGH3N.1/03/11.b2, 16EHLOW2N.1/03/11.b1, 4EHHIGH1P.1/03/11.b1, 39EHHIGH1N.3/06/11.b1, 7EHHIGH3N.3/11/11.b1, 7EHHIGH3P.3/11/11.b1, 7EHLOW2P.3/11/11.b3, 47ECLOW4N.3/13/11.b2, 47EHHIGH1P.3/15/11.b1, 47EHHIGH1P.3/15/11.b2, 47EHHIGH3P.3/15/11.b1, 17EHHIGH1N.3/18/11.b3, 17EHHIGH1P.3/18/11.b1, 17EHLOW2N.3/18/11.b2, 17EHLOW4P.3/18/11.b2, 4EHHIGH1N.3/19/11.b1, 4EHHIGH1N.3/19/11.b5, 4EHHIGH1N.3/19/11.b6, 4EHHIGH3N.3/19/11.b1, 4EHHIGH3N.3/19/11.b2, 4EHHIGH3N.3/19/11.b4, 4EHLOW2N.3/19/11.b4, 4EHLOW2P.3/19/11.b1, 4EHLOW2P.3/19/11.b2, 4EHLOW2P.3/19/11.b4, 4EHLOW2P.3/19/11.b6, 46EHHIGH3P.3/20/11.b1, 46ECLOW4P.3/21/11.b3, 16EHHIGH1N.3/22/11.b1, 16EHHIGH1N.3/22/11.b2, 16EHHIGH1N.3/22/11.b3, 16EHHIGH1N.3/22/11.b4, 16EHHIGH1N.3/22/11.b5, 16EHHIGH1P.3/22/11.b1, 16EHHIGH3N.3/22/11.b10, 16EHHIGH3N.3/22/11.b11, 16EHHIGH3N.3/22/11.b12, 16EHHIGH3N.3/22/11.b14, 16EHHIGH3N.3/22/11.b16, 16EHHIGH3N.3/22/11.b17, 16EHHIGH3N.3/22/11.b18, 16EHHIGH3N.3/22/11.b19, 16EHHIGH3N.3/22/11.b2, 16EHHIGH3N.3/22/11.b20, 16EHHIGH3N.3/22/11.b21, 16EHHIGH3N.3/22/11.b22, 16EHHIGH3N.3/22/11.b23, 16EHHIGH3N.3/22/11.b24, 16EHHIGH3N.3/22/11.b4, 16EHHIGH3N.3/22/11.b5, 16EHHIGH3N.3/22/11.b5, 16EHHIGH3N.3/22/11.b6, 16EHHIGH3N.3/22/11.b7, 16EHHIGH3N.3/22/11.b8, 16EHHIGH3N.3/22/11.b9, 16EHHIGH3N.3/22/11.b1, 16EHHIGH3P.3/22/11.b1, 16EHHIGH3P.3/22/11.b10, 16EHHIGH3P.3/22/11.b2, 16EHHIGH3P.3/22/11.b3, 16EHHIGH3P.3/22/11.b4, 16EHHIGH3P.3/22/11.b5, 16EHHIGH3P.3/22/11.b6, 16EHHIGH3P.3/22/11.b8, 16EHHIGH3P.3/22/11.b9, 16EHLOW2N.3/22/11.b1, 16EHLOW2N.3/22/11.b2, 16EHLOW2N.3/22/11.b3, 16EHLOW2N.3/22/11.b4, 16EHLOW2N.3/22/11.b6, 16EHLOW2P.3/22/11.b1, 16EHLOW2P.3/22/11.b2, 16EHLOW2P.3/22/11.b4, 16EHLOW2P.3/22/11.b6, 16EHLOW4N.3/22/11.b1, 16EHLOW4N.3/22/11.b2, 16EHLOW4N.3/22/11.b3, 16EHLOW4P.3/22/11.b1, 16EHLOW4P.3/22/11.b4, 4ECHIGH1N.3/23/11.b1, 4ECHIGH1P.3/23/11.b1, 4ECHIGH1P.3/23/11.b2, 4ECHIGH1P.3/23/11.b3, 4ECHIGH1P.3/23/11.b4, 4ECLOW2P.3/23/11.b1, 4ECLOW2P.3/23/11.b2, 4ECLOW4N.3/23/11.b1, 4ECLOW4N.3/23/11.b3, 4ECLOW4N.3/23/11.b5, 4ECLOW4N.3/23/11.b6, 4ECLOW4P.3/23/11.b1, 4ECLOW4P.3/23/11.b10, 4ECLOW4P.3/23/11.b2, 4ECLOW4P.3/23/11.b4, 4ECLOW4P.3/23/11.b5, 4ECLOW4P.3/23/11.b7, 4ECLOW4P.3/23/11.b8, 4ECLOW4P.3/23/11.b9, 4ECHIGH1P.5/09/11.b1, 4EHHIGH1P.5/10/11.b2, 4ECLOW2P.1/28/11.b1, 16EHHIGH3P.2/06/11.b1, 4ECLOW4P.2/14/11.b1, 4ECLOW4P.2/14/11.b2
	Agathidinae sp. 1.m	39EHHIGH3P.2/01/11.b2
Alysiinae	Alysiinae sp.	39ECLOW2P.10/21/10.b3, 4EHLOW4P.10/31/10.b1, 4EHLOW4P.10/31/10.b2, 39ECLOW2N.11/17/10.b1, 47ECLOW2N.11/29/10.b2, 47ECLOW2P.11/29/10.b2, 47ECLOW4P.11/29/10.b1, 46ECLOW2N.12/02/10.b1, 12EHHIGH1P.12/31/10.b1, 12EHLOW4N.12/31/10.b6, 12EHLOW4N.12/31/10.b9, 39ECHIGH1P.12/31/10.b3, 39EHHIGH3P.12/31/10.b3, 39EHLOW2P.12/31/10.b2, 12ECLOW4P.1/01/11.b1, 4ECLOW4N.1/02/11.b1, 4ECLOW4P.1/02/11.b1, 4ECLOW4P.1/02/11.b4, 4ECLOW4P.1/02/11.b9, 7EHLOW2N.1/02/11.b3, 16ECHIGH3P.1/03/11.b2, 16EHHIGH3N.1/03/11.b3, 4EHHIGH3N.1/03/11.b1, 4EHHIGH3N.1/03/11.b3, 4EHLOW4P.1/03/11.b3, 17ECHIGH3P.1/05/11.i1, 17ECLOW2N.1/05/11.b4, 17ECLOW4N.1/05/11.b2, 17ECLOW4P.1/05/11.b1, 17ECLOW4P.1/05/11.b4, 17ECLOW4P.1/05/11.b5, 17ECLOW4P.1/05/11.b6, 17EHLOW2P.1/05/11.b1, 17EHLOW4P.1/05/11.b1, 46ECHIGH1P.1/06/11.b1, 46ECHIGH1P.1/06/11.b2, 46ECHIGH3P.1/06/11.b1, 46EHLOW2P.1/06/11.b1, 47ECLOW4P.1/07/11.b1, 39EHLOW2N.1/11/11.b1, 39ECLOW2P.1/13/11.b1, 12ECHIGH1P.1/15/11.b1, 12ECLOW2P.1/15/11.b1, 17EHHIGH3P.1/20/11.b2, 47ECLOW2N.1/25/11.b1, 47EHLOW4P.1/25/11.b5, 17ECLOW2N.1/27/11.b1, 17ECLOW4P.1/27/11.b10, 17ECLOW4P.1/27/11.b11, 17ECLOW4P.1/27/11.b12, 17ECLOW4P.1/27/11.b7, 39ECLOW4N.2/02/11.b2, 39ECLOW4P.2/02/11.b5, 12ECHIGH1P.2/03/11.b1, 12ECHIGH3N.2/03/11.b1, 12EHLOW4P.2/04/11.b2, 16ECHIGH1N.2/06/11.i1, 16ECHIGH3N.2/06/11.b1, 16ECLOW4N.2/06/11.b1, 16EHHIGH1P.2/06/11.b1, 47ECLOW2N.2/09/11.b1, 47ECLOW2P.2/09/11.b1, 7ECLOW2P.2/09/11.b1, 46EHLOW4P.2/11/11.b1, 17EHLOW4N.2/12/11.b3, 17EHLOW4N.2/12/11.b4, 4EHHIGH3P.2/15/11.b1, 4EHLOW2P.2/15/11.b2, 4EHLOW2P.2/15/11.b4, 12EHHIGH3N.3/06/11.b2, 12EHLOW2P.3/06/11.b10, 12EHLOW2P.3/06/11.b5, 39EHHIGH3P.3/06/11.b1, 39EHLOW2P.3/06/11.b5, 39EHLOW4N.3/06/11.b1, 12ECHIGH1N.3/08/11.b1, 39ECHIGH3P.3/10/11.b2, 39ECHIGH3P.3/10/11.b6, 39ECLOW2N.3/10/11.b2, 7EHHIGH3P.3/11/11.b1, 47ECLOW2N.3/13/11.b1, 47ECLOW2N.3/13/11.b2, 47ECLOW2P.3/13/11.b1, 47ECLOW4N.3/13/11.b1, 47ECLOW4N.3/13/11.b3, 16ECHIGH3P.3/14/11.b5, 16ECLOW2P.3/14/11.b2, 16ECLOW2P.3/14/11.b3, 16ECLOW2P.3/14/11.b4, 16ECLOW2P.3/14/11.b5, 47EHHIGH1P.3/15/11.b4, 47EHHIGH1P.3/15/11.b5, 47EHLOW2N.3/15/11.b1, 47EHLOW2P.3/15/11.b1, 47EHLOW4P.3/15/11.b3, 17ECHIGH1P.3/17/11.b1, 17ECLOW2N.3/17/11.b1, 17ECLOW4P.3/17/11.b11, 17ECLOW4P.3/17/11.b7, 17ECLOW4P.3/17/11.b8, 17EHHIGH1N.3/18/11.b4, 17EHHIGH1N.3/18/11.b5, 17EHHIGH1N.3/18/11.b6, 17EHHIGH3N.3/18/11.b1, 17EHHIGH3N.3/18/11.b2, 17EHHIGH3P.3/18/11.b1, 17EHLOW2N.3/18/11.b1, 17EHLOW4N.3/18/11.b1, 17EHLOW4N.3/18/11.b3, 17EHLOW4P.3/18/11.b1, 4EHHIGH1N.3/19/11.b2, 4EHHIGH1N.3/19/11.b4, 4EHHIGH1N.3/19/11.b7, 4EHHIGH1N.3/19/11.b8, 4EHHIGH1N.3/19/11.b9, 4EHHIGH1P.3/19/11.b1, 4EHHIGH1P.3/19/11.b3, 4EHHIGH3N.3/19/11.b3, 4EHHIGH3N.3/19/11.b5, 4EHHIGH3N.3/19/11.b6, 4EHHIGH3N.3/19/11.b7, 4EHHIGH3P.3/19/11.b1, 4EHLOW2N.3/19/11.b1, 4EHLOW2N.3/19/11.b2, 4EHLOW2N.3/19/11.b3, 4EHLOW2N.3/19/11.b5, 4EHLOW2P.3/19/11.b3, 4EHLOW2P.3/19/11.b5, 4EHLOW4P.3/19/11.b2, 46EHHIGH1N.3/20/11.b1, 46EHHIGH1N.3/20/11.b2, 46EHHIGH1P.3/20/11.b1, 46EHHIGH1P.3/20/11.b2, 46EHHIGH1P.3/20/11.b3, 46EHHIGH1P.3/20/11.b4, 46EHHIGH3P.3/20/11.b2, 46EHHIGH3P.3/20/11.b3, 46EHHIGH3P.3/20/11.b4, 46EHLOW2P.3/20/11.b1, 46ECHIGH1P.3/21/11.b1, 46ECHIGH1P.3/21/11.b2, 46ECHIGH3P.3/21/11.b3, 46ECLOW2P.3/21/11.b1, 46ECLOW4P.3/21/11.b1, 46ECLOW4P.3/21/11.b2, 46ECLOW4P.3/21/11.b4, 46ECLOW4P.3/21/11.b5, 46ECLOW4P.3/21/11.b6, 16EHHIGH3N.3/22/11.b13, 16EHHIGH3N.3/22/11.b3, 16EHLOW2N.3/22/11.b7, 16EHLOW2P.3/22/11.b5, 16EHLOW2P.3/22/11.b7, 16EHLOW4N.3/22/11.b4, 16EHLOW4P.3/22/11.b2, 16EHLOW4P.3/22/11.b3, 4ECLOW4P.3/23/11.b6, 12ECHIGH3P.5/04/11.b1, 12ECLOW2P.5/04/11.b1, 12ECLOW4N.5/04/11.b1, 12ECLOW4P.5/04/11.b1, 12EHHIGH1P.5/04/11.b1, 12EHLOW2P.5/04/11.b1, 12EHLOW4N.5/04/11.b3, 12EHLOW4P.5/04/11.b1, 39ECLOW2N.5/05/11.b1, 39ECLOW2P.5/05/11.b2, 39ECLOW4N.5/05/11.b1, 39EHHIGH1N.5/05/11.b1, 39EHHIGH1P.5/05/11.b3, 39EHHIGH1P.5/05/11.b4, 39EHHIGH3N.5/05/11.b1, 39EHLOW2N.5/05/11.b4, 39EHLOW2P.5/05/11.b1, 39EHLOW2P.5/05/11.b3, 39EHLOW2P.5/05/11.b4, 7ECHIGH3P.5/06/11.b1, 7EHHIGH1P.5/06/11.b1, 7EHHIGH1P.5/06/11.b2, 7EHLOW2P.5/06/11.b1,

		46ECHIGH3P.5/08/11.b1, 46ECLOW2P.5/08/11.b1, 46ECLOW2P.5/08/11.b2, 46ECLOW4P.5/08/11.b1, 46EHHIGH1N.5/08/11.b1, 46EHHIGH1N.5/08/11.b2, 46EHHIGH1N.5/08/11.b3, 46EHHIGH1P.5/08/11.b1, 46EHHIGH1P.5/08/11.b2, 46EHHIGH1P.5/08/11.b3, 46EHHIGH1P.5/08/11.b4, 46EHHIGH1P.5/08/11.b5, 46EHHIGH1P.5/08/11.b6, 46EHHIGH3N.5/08/11.b1, 46EHHIGH3N.5/08/11.b2, 46EHHIGH3P.5/08/11.b1, 46EHHIGH3P.5/08/11.b2, 46EHLOW4P.5/08/11.b1, 46EHLOW4P.5/08/11.b2, 4ECHIGH1P.5/09/11.b2, 4ECLOW2P.5/09/11.b1, 4ECLOW2P.5/09/11.b2, 4ECLOW2P.5/09/11.b3, 4ECLOW2P.5/09/11.b4, 4ECLOW2P.5/09/11.b5, 16ECHIGH1P.5/10/11.b3, 16ECLOW2N.5/10/11.b2, 16ECLOW2P.5/10/11.b10, 16ECLOW2P.5/10/11.b13, 16ECLOW2P.5/10/11.b8, 16ECLOW4P.5/10/11.b7, 16ECLOW4P.5/10/11.b8, 4EHHIGH1N.5/10/11.b1, 4EHHIGH1N.5/10/11.b2, 4EHHIGH1N.5/10/11.b3, 4EHHIGH1N.5/10/11.b4, 4EHHIGH1P.5/10/11.b1, 4EHHIGH1P.5/10/11.b3, 4EHHIGH1P.5/10/11.b4, 4EHHIGH1P.5/10/11.b5, 4EHHIGH1P.5/10/11.b6, 4EHHIGH1P.5/10/11.b7, 4EHHIGH3N.5/10/11.b2, 4EHHIGH3N.5/10/11.b3, 4EHHIGH3N.5/10/11.b4, 4EHHIGH3P.5/10/11.b1, 4EHHIGH3P.5/10/11.b2, 4EHHIGH3P.5/10/11.b3, 4EHHIGH3P.5/10/11.b4, 4EHHIGH3P.5/10/11.b5, 4EHLOW2P.5/10/11.b1, 4EHLOW2P.5/10/11.b10, 4EHLOW2P.5/10/11.b11, 4EHLOW2P.5/10/11.b12, 4EHLOW2P.5/10/11.b14, 4EHLOW2P.5/10/11.b15, 4EHLOW2P.5/10/11.b16, 4EHLOW2P.5/10/11.b17, 4EHLOW2P.5/10/11.b18, 4EHLOW2P.5/10/11.b19, 4EHLOW2P.5/10/11.b20, 4EHLOW2P.5/10/11.b4, 4EHLOW2P.5/10/11.b6, 4EHLOW2P.5/10/11.b7, 4EHLOW2P.5/10/11.b8, 4EHLOW2P.5/10/11.b9, 4EHLOW4P.5/10/11.b2, 4EHLOW4P.5/10/11.b3, 4EHLOW4P.5/10/11.b4, 4EHLOW4P.5/10/11.b5, 4EHLOW4P.5/10/11.b6, 4EHLOW4P.5/10/11.b7, 4EHLOW4P.5/10/11.b8, 4EHLOW4P.5/10/11.b9, 17ECHIGH1P.5/11/11.b1, 17EHLOW4P.5/11/11.b1, 47ECHIGH3N.5/12/11.b2, 47EHHIGH1P.5/12/11.b1, 47EHHIGH1P.5/12/11.b3, 47EHLOW4N.5/12/11.b1, 47EHLOW4P.5/12/11.b3, 47EHLOW4P.5/12/11.b5
Aphidiinae	Aphidiinae sp.	39ECLOW4P.1/13/11.b3, 39ECHIGH3P.3/10/11.b1, 39ECLOW4P.3/10/11.b1, 39ECLOW4P.3/10/11.b5
Cheloninae	Cheloninae black	17ECLOW4P.1/27/11.b8, 17ECLOW4P.1/27/11.b9, 12EHLOW4N.2/04/11.b9, 12ECLOW4N.3/08/11.b2, 46ECHIGH3P.3/21/11.b1
	Cheloninae brown head	17ECLOW4P.1/05/11.b7, 47EHLOW4P.1/07/11.b3, 17ECLOW4P.1/27/11.b5, 39ECLOW4P.2/02/11.b4, 39EHLOW2P.3/06/11.b1, 39EHLOW2P.3/06/11.b2, 39ECLOW4P.3/10/11.b3, 7ECLOW4P.3/12/11.b1, 47EHHIGH3P.3/15/11.b2
	Cheloninae mottled	12EHLOW4N.12/31/10.b2, 12EHLOW4N.12/31/10.b4, 12EHLOW4N.12/31/10.b5, 39ECLOW2N.12/31/10.b3, 39ECLOW4P.12/31/10.b2, 4EHLOW2P.1/03/11.b3, 4EHLOW4P.1/03/11.b1, 12EHLOW4N.1/10/11.b1, 12EHLOW4N.1/10/11.b2, 12EHLOW4N.1/10/11.b3, 12EHLOW4N.1/10/11.b4, 12EHLOW4N.1/10/11.b7, 39EHLOW2P.1/11/11.b1, 39ECHIGH1N.1/13/11.b1, 39ECLOW2P.1/13/11.b3, 12ECLOW2N.1/15/11.b1, 17EHHIGH1P.1/20/11.b1, 17EHHIGH1P.1/20/11.b2, 17EHLOW4N.1/20/11.b2, 17EHLOW4N.1/20/11.b4, 17EHLOW4P.1/20/11.b1, 17EHLOW4P.1/20/11.b2, 17EHLOW4P.1/20/11.b3, 7ECHIGH1N.1/21/11.b1, 7ECLOW4N.1/21/11.b1, 4EHLOW4P.1/24/11.b1, 17ECLOW2P.1/27/11.b1, 17ECLOW4P.1/27/11.b1, 17ECLOW4P.1/27/11.b6, 39ECLOW4P.2/02/11.b1, 12EHHIGH3N.2/04/11.b1, 12EHHIGH3N.2/04/11.b2, 12EHHIGH3P.2/04/11.b1, 12EHHIGH3P.2/04/11.b2, 12EHLOW4N.2/04/11.b1, 12EHLOW4N.2/04/11.b10, 12EHLOW4N.2/04/11.b11, 12EHLOW4N.2/04/11.b2, 12EHLOW4N.2/04/11.b3, 12EHLOW4N.2/04/11.b4, 12EHLOW4N.2/04/11.b6, 12EHLOW4N.2/04/11.b7, 7ECHIGH3P.2/09/11.b1, 7ECLOW4N.2/09/11.b2, 7ECLOW4P.2/09/11.b1, 17EHHIGH1P.2/12/11.b1, 17EHLOW4N.2/12/11.b2, 17EHLOW4P.2/12/11.b1, 17EHLOW4P.2/12/11.b2, 17ECHIGH3N.2/13/11.b1, 17ECLOW2P.2/13/11.b2, 17ECLOW2P.2/13/11.b3, 17ECLOW2P.2/13/11.b4 , 17ECLOW4N.2/13/11.b1, 17ECLOW4P.2/13/11.b2, 17ECLOW4P.2/13/11.b3, 17ECLOW4P.2/13/11.b6, 12EHHIGH1P.3/06/11.b1, 12EHHIGH3N.3/06/11.b1, 12EHHIGH3N.3/06/11.b3, 12EHHIGH3N.3/06/11.b4, 12EHLOW2N.3/06/11.b1, 12EHLOW2P.3/06/11.b1, 12EHLOW2P.3/06/11.b2, 12EHLOW2P.3/06/11.b3, 12EHLOW2P.3/06/11.b4, 12EHLOW2P.3/06/11.b6, 12EHLOW2P.3/06/11.b7, 12EHLOW2P.3/06/11.b9, 12EHLOW4N.3/06/11.b1, 12EHLOW4N.3/06/11.b2, 12EHLOW4N.3/06/11.b6, 12EHLOW4N.3/06/11.b7, 12ECHIGH1N.3/08/11.b2, 12ECLOW4N.3/08/11.b1, 7EHLOW4P.3/11/11.b1, 7ECLOW2P.3/12/11.b1, 47EHLOW4P.3/15/11.b2, 17ECLOW4N.3/17/11.b1, 17ECLOW4P.3/17/11.b1, 17ECLOW4P.3/17/11.b2, 17ECLOW4P.3/17/11.b4, 17ECLOW4P.3/17/11.b5, 17EHHIGH1N.3/18/11.b1, 17EHHIGH1N.3/18/11.b2, 17EHHIGH1P.3/18/11.b2, 12EHHIGH1P.5/04/11.b2, 12EHHIGH3P.5/04/11.b1, 17ECLOW4P.5/11/11.b1
Dirrhopinae	Dirrhopinae sp. 1	39ECHIGH3P.12/31/10.b3
Doryctinae	Doryctinae sp.	39EHLOW2P.11/16/10.b2, 16EHLOW2N.11/21/10.b1, 17EHLOW2P.11/24/10.b1, 47ECLOW2P.11/29/10.b1, 4EHLOW2P.11/30/10.b1, 39EHHIGH1P.12/31/10.b1, 4ECLOW4P.1/02/11.b5, 4ECLOW2P.1/02/11.b4, 4ECLOW4P.1/02/11.b8, 4EHLOW2P.1/03/11.b2, 17EHLOW2N.1/05/11.b1, 47ECLOW2P.1/07/11.b1, 47EHHIGH3P.1/07/11.b2, 39ECHIGH1P.1/13/11.b1, 47ECLOW4N.1/25/11.b2, 47EHLOW4P.1/25/11.b6, 4ECHIGH3P.2/14/11.b1, 4EHHIGH1N.2/15/11.b1, 39EHLOW2P.3/06/11.b4, 7EHLOW2P.3/11/11.b2, 47ECLOW2P.3/13/11.b2, 16ECLOW2P.3/14/11.b2, 17EHHIGH3P.3/18/11.b1, 4ECLOW4N.3/23/11.b2, 39EHHIGH3P.5/05/11.b1, 4ECHIGH3P.5/09/11.b1, 47ECLOW4N.5/12/11.b2, 47EHHIGH1N.5/12/11.b1, 47EHHIGH1P.5/12/11.b2, 47EHLOW4P.5/12/11.b4
Euphorinae	Euphorinae sp.	39EHLOW2P.11/16/10.b3, 39ECHIGH1P.12/31/10.b4, 39EHLOW2N.12/31/10.b3, 16EHLOW2P.1/03/11.b1, 39ECLOW2P.1/13/11.b4, 12ECLOW4P.1/15/11.b1, 17EHLOW4N.1/20/11.b1, 39EHLOW4N.2/01/11.b1, 39ECHIGH3P.2/02/11.b2, 12EHLOW4P.2/04/11.b1, 16ECLOW2N.2/06/11.b1, 16EHHIGH1P.2/06/11.b2, 17EHLOW4N.2/12/11.b5, 12EHLOW4N.3/06/11.b9, 12EHLOW4P.3/06/11.b1, 39EHHIGH3P.3/06/11.b3, 12ECLOW2N.3/08/11.b1, 12ECLOW4N.3/08/11.b3, 39ECLOW4N.3/10/11.b1, 39ECLOW2P.5/05/11.b1, 39EHHIGH3P.5/05/11.b2
Helconinae	Brachistini sp.	17ECLOW2N.1/05/11.b5, 17ECLOW2N.1/05/11.b6, 46ECLOW4P.1/06/11.b2, 39ECLOW4P.2/02/11.b3, 17ECLOW2N.2/13/11.b1, 17ECLOW2N.2/13/11.b4, 17ECLOW4P.2/13/11.b4, 17ECLOW4P.2/13/11.b5, 17ECLOW4P.2/13/11.b7, 4ECLOW4P.2/14/11.b3, 39ECLOW4P.3/10/11.b4, 17ECLOW4P.3/17/11.b10, 17ECLOW4P.3/17/11.b3, 17EHLOW4N.3/18/11.b4, 17ECLOW4P.5/11/11.b3
Homolobinae	Homolobinae sp.	17ECLOW4P.1/27/11.b3, 17ECLOW4P.1/27/11.b4, 17ECLOW4P.2/13/11.b1
Ichneutinae	Ichneutinae sp.	12EHLOW4N.12/31/10.b3, 4ECLOW4P.1/02/11.b3, 16ECLOW4P.1/17/11.b1
Meteoridiinae	Meteoridinae sp. 1	16ECLOW4P.5/10/11.b6, 7ECHIGH1P.3/12/11.b1, 12EHLOW4N.5/04/11.b2, 39EHHIGH1P.5/05/11.b2, 39EHLOW2N.5/05/11.b5, 7ECHIGH1P.5/06/11.b1, 16ECLOW2P.5/10/11.b7, 16ECHIGH1P.5/10/11.b1, 16ECHIGH1P.5/10/11.b2, 16ECLOW2N.5/10/11.b4, 16ECLOW4N.5/10/11.b1
	Meteoridinae sp. 2	16ECLOW4P.1/03/11.b2
	Meteoridinae sp. 3	16ECHIGH1P.5/10/11.b4
	Meteoridinae sp. 4	47EHLOW2P.1/25/11.b2
	Meteoridinae sp.m	16ECLOW2P.3/14/11.b1, 16ECHIGH3P.3/14/11.b3
Meteorinae	Meteorinae long ovipositor	4ECLOW2P.12/01/10.b1, 17ECLOW2N.1/05/11.b2, 46ECLOW4P.1/06/11.b3, 47ECLOW4P.1/07/11.b2, 47ECLOW4P.1/25/11.b1, 12EHLOW4N.3/06/11.b3, 12EHLOW4N.3/06/11.b5, 17ECLOW4P.3/17/11.b6, 4ECLOW4P.5/09/11.b1, 16ECLOW2N.5/10/11.b3
	Meteorinae sp.	17ECLOW2N.1/05/11.b3, 46ECLOW4P.1/06/11.b4, 16ECLOW2P.5/10/11.b3

	Meteorus annettae	7EHHIGH3N.11/26/10.b1
	Meteorus cespitator	16EHHIGH3P.11/21/10.b1, 7EHHIGH1N.1/02/11.b1, 47EHHIGH1N.2/08/11.b2
	Meteorus luteus	47EHHIGH3P.11/27/10.b1, 46EHHIGH3P.12/02/10.b1
	Meteorus novazealandicus	12EHLOW4N.11/19/10.b1, 16EHLOW2P.11/21/10.b1, 16EHLOW4P.11/21/10.b1, 47ECLOW2N.11/29/10.b1, 46ECHIGH3P.12/02/10.b1, 12EHLOW4N.12/31/10.b1, 39ECLOW2N.12/31/10.b1, 39ECLOW4N.12/31/10.b1, 39EHHIGH3P.12/31/10.b2, 12ECLOW2P.1/01/11.b1, 12ECLOW4N.1/01/11.b2, 7ECLOW4N.1/01/11.b1, 4ECLOW2P.1/02/11.b2, 4ECLOW4P.1/02/11.b2, 46EHHIGH1P.1/06/11.b1, 46EHHIGH3P.1/06/11.b1, 47EHHIGH3P.1/07/11.b4, 47EHLOW2P.1/07/11.b1, 47EHLOW2P.1/07/11.b3, 47ECLOW2P.1/25/11.b1, 47ECLOW4N.1/25/11.b1, 47EHHIGH3P.1/25/11.b1, 47EHLOW4P.1/25/11.b3, 47EHLOW4P.1/25/11.b1, 39EHHIGH3P.2/01/11.b1, 47EHHIGH1N.2/08/11.b1, 7ECLOW4N.2/09/11.b1, 17EHLOW2P.2/12/11.b1, 12EHLOW4N.3/06/11.b4
	Meteorus pulchricornis	39ECHIGH3P.12/31/10.b1, 16ECHIGH3P.3/14/11.b1
Microgastrinae	*Choeras* large sp.	39EHHIGH1P.11/16/10.b1, 39ECHIGH3N.11/17/10.b1, 12EHHIGH3N.11/19/10.b1, 7EHLOW2P.11/26/10.b4, 47EHLOW4P.11/27/10.b1, 47ECLOW4N.11/29/10.b1, 7ECLOW2P.1/01/11.b1, 7EHLOW2N.1/02/11.b2, 17ECHIGH3N.1/05/11.b1, 17ECHIGH3N.1/05/11.b2, 17ECHIGH3P.1/05/11.i2, 17ECLOW2N.1/05/11.b1, 17ECLOW4P.1/05/11.b2, 17ECLOW4P.1/05/11.b3, 17ECHIGH3P.1/27/11.b1, 4ECLOW4P.1/28/11.b1, 39ECHIGH3N.2/02/11.b1, 39EHLOW2P.3/06/11.b3
	Choeras sp.	39ECHIGH1P.12/31/10.b1, 39ECHIGH1P.12/31/10.b2, 39ECLOW4P.12/31/10.b4, 4ECLOW2P.1/02/11.b1, 4ECLOW2P.1/02/11.b5, 47EHLOW4P.1/07/11.b1, , 12EHLOW4N.1/10/11.b5, 39ECLOW4P.1/13/11.b2, 47ECLOW2N.1/25/11.b2, 16ECHIGH3P.2/06/11.b1, 47EHHIGH1P.2/08/11.b1, 46EHHIGH1P.2/11/11.b1, 39EHLOW4P.3/06/11.b1, 12ECLOW4P.3/08/11.b1, 39ECHIGH3P.3/10/11.b4, 39ECLOW4P.3/10/11.b2, 7ECLOW4N.3/12/11.b2, 16ECHIGH3N.3/14/11.b1, 16ECHIGH3N.3/14/11.b2, 16ECHIGH3P.3/14/11.b4, 47EHLOW4P.3/15/11.b1, 7EHLOW2P.5/06/11.b4, 16ECHIGH3N.5/10/11.b1, 16ECLOW2N.5/10/11.b1, 16ECLOW2P.5/10/11.b6, 4EHLOW4P.5/10/11.b1, 47ECHIGH3P.5/12/11.b1, 47EHLOW4P.5/12/11.b1
	Cotesia sp.	17EHLOW4N.11/24/10.b1, 16ECLOW2P.2/06/11.b2, 17ECLOW2P.2/13/11.b1, 4EHHIGH1P.2/15/11.b1, 12ECHIGH1N.3/08/11.b3, 7EHHIGH1N.3/11/11.b1, 7EHHIGH1P.3/11/11.b1, 7ECLOW2P.3/12/11.b2, 17EHHIGH1N.3/18/11.b3, 17EHLOW4N.3/18/11.b2, 16EHHIGH3P.3/22/11.b7
	Dolichogenidea brown mesoscutum	4EHHIGH1N.3/19/11.b3
	Dolichogenidea patterned mesoscutum	7EHLOW4P.5/06/11.b1
	Dolichogenidea darklegs sp. 4	39ECHIGH3P.12/31/10.b2, 39ECLOW2P.2/02/11.b1, 12ECLOW2P.2/03/11.b1, 47EHHIGH1P.3/15/11.b3, 12ECLOW2N.5/04/11.b2
	Dolichogenidea lightly punct.	12ECLOW2N.1/01/11.b2, 39ECLOW2N.1/13/11.b1, 46EHLOW2P.1/26/11.b1, 39EHHIGH1N.2/01/11.b1
	Glyptapanteles sp. 2	39ECLOW4P.12/31/10.b3, 39ECLOW4P.12/31/10.b5, 47EHLOW4P.1/25/11.b2, 47EHHIGH3P.5/12/11.b1
	Glyptapanteles sp. 3	16ECLOW4P.1/03/11.b1, 39ECLOW4P.3/10/11.b6, 39EHLOW2P.5/05/11.b5
	Glyptapanteles sp. 4	39ECHIGH3P.12/31/10.b4, 39ECLOW4P.12/31/10.b1, 39EHLOW2N.12/31/10.b4, 39EHLOW2P.12/31/10.b1, 7ECLOW4P.1/01/11.b2, 17EHLOW4N.1/05/11.b1, 39ECHIGH3P.2/02/11.b1, 12ECLOW2N.2/03/11.b1, 12EHLOW4P.2/04/11.b3, 16ECLOW2P.5/10/11.b9, 17ECLOW4P.5/11/11.b2
	Microgastrinae sp.	12ECLOW2P.1/01/11.b2, 39ECHIGH1N.2/02/11.b1, 12ECLOW4P.3/08/11.b2
Opiinae	Opiinae sp.	16EHLOW4N.11/21/10.b1, 17ECLOW2N.1/05/11.b7, 47ECLOW4P.1/07/11.b6, 47EHHIGH3N.1/07/11.b1, 39EHHIGH1P.5/05/11.b5, 39EHLOW2N.5/05/11.b2, 7EHLOW2P.5/06/11.b9, 4ECLOW4P.5/09/11.b2, 16ECLOW2P.5/10/11.b12
Rogadinae	*Aleiodes* sp.	39EHHIGH3N.12/31/10.b1, 7ECLOW2N.1/01/11.b1, 7EHHIGH1P.1/02/11.b1, 17EHHIGH3N.1/05/11.b1, 47EHHIGH3P.1/07/11.b1, 47ECHIGH3N.1/25/11.b1, 4EHLOW4P.3/19/11.b1, 16ECLOW2P.5/10/11.b1, 16ECLOW4N.5/10/11.b2, 16ECLOW4P.5/10/11.b1, 16ECLOW4P.5/10/11.b2, 47ECLOW4P.5/12/11.b3, 47ECLOW4P.5/12/11.b4
	Rogadinae brown, uneven stigma	4ECLOW2P.1/02/11.b3, 4ECLOW4P.1/02/11.b7, 4EHHIGH3N.1/03/11.b2, 47ECHIGH3P.1/07/11.b1, 39EHLOW2N.2/01/11.b1, 47ECLOW4P.2/09/11.b1, 17ECLOW2N.2/13/11.b3, 4EHLOW4N.2/15/11.b1, 39EHLOW4P.3/06/11.b2, 16ECLOW2P.3/14/11.b1, 4ECLOW4N.3/23/11.b4, 4ECLOW4P.3/23/11.b11, 39EHHIGH1P.5/05/11.b1, 4EHHIGH3N.5/10/11.b1
	Rogadinae brown, white legs	16ECLOW4P.10/14/10.b1, 39ECLOW2P.10/21/10.b2, 7EHLOW2N.10/22/10.b1, 39EHLOW2P.11/16/10.b1, 7EHLOW2N.11/26/10.b1, 7EHLOW2P.11/26/10.b2, 46ECLOW4P.12/02/10.b1, 12EHLOW4N.12/31/10.b8, 12EHLOW4P.12/31/10.b1, 39EHHIGH3P.12/31/10.b1, 12ECLOW2N.1/01/11.b1, 4ECLOW2P.1/02/11.b6, 7EHLOW2P.1/02/11.b1, 16ECHIGH3N.1/03/11.b1, 16ECLOW2P.1/03/11.b1, 4EHLOW4P.1/03/11.b4, 46ECLOW4P.1/06/11.b1, 47EHLOW2P.1/07/11.b2, 12EHLOW4N.2/04/11.b8, 47EHHIGH3P.2/08/11.b1, 4EHLOW2P.2/15/11.b1, 12EHHIGH1N.3/06/11.b1, 12EHLOW2P.3/06/11.b8, 12EHLOW4N.3/06/11.b8, 39EHHIGH1P.3/06/11.b1, 39EHLOW2N.3/06/11.b1, 16ECLOW2P.5/10/11.b2, 16ECLOW4N.5/10/11.b3, 4EHLOW2N.5/10/11.b1, 4EHLOW2P.5/10/11.b2
	Rogadinae cavern face	39EHLOW2N.12/31/10.b1, 4EHLOW2P.1/03/11.b1, 39EHHIGH1N.2/01/11.b2, 39EHLOW2P.5/05/11.b2
	Rogadinae long ovipositor	16ECLOW4N.1/03/11.b1, 4EHLOW4P.1/03/11.b2, 7ECHIGH3P.3/12/11.b1, 16ECHIGH3P.3/14/11.b2
	Rogadinae long thin.m	39ECLOW2P.10/21/10.b1, 7EHLOW2N.10/22/10.b2, 39EHLOW2N.11/16/10.b1, 39ECLOW4P.11/17/10.b1, 12EHLOW4N.11/19/10.b2, 7ECLOW4N.11/25/10.b2, 7EHLOW2N.11/26/10.b2, 7EHLOW2P.11/26/10.b1, 7EHLOW2P.11/26/10.b3, 7EHLOW2P.11/26/10.b5, 47ECLOW4N.11/29/10.b2, 47ECLOW4N.11/29/10.b3, 4ECLOW4P.12/01/10.b1, 39EHLOW2P.12/31/10.b7, 39EHLOW2P.12/31/10.b8, 47ECLOW4P.1/07/11.b4, 12EHLOW4N.1/10/11.b8, 39EHLOW2P.1/11/11.b3, 39EHLOW2P.1/11/11.b5, 17EHLOW4N.1/20/11.b3, 17EHLOW4N.1/20/11.b5, 47EHLOW2P.1/25/11.b1, 47EHLOW4P.1/25/11.b4, 16ECLOW2P.2/06/11.b1, 17EHHIGH3P.2/12/11.b1, 17EHHIGH3P.2/12/11.b2, 17EHLOW4N.2/12/11.b1, 4EHLOW2P.2/15/11.b3, 39EHHIGH3P.3/06/11.b2, 47ECLOW4P.3/13/11.b1, 39ECHIGH3P.5/05/11.b1, 16ECLOW4P.5/10/11.b4, 4EHLOW2P.5/10/11.b13, 4EHLOW2P.5/10/11.b3, 17EHLOW4N.5/11/11.b1, 17EHLOW4P.5/11/11.b2, 47ECLOW2P.5/12/11.b1, 47EHLOW4P.5/12/11.b2
	Rogadinae shiny brown head	4ECLOW4P.2/14/11.b4,
	Rogadinae small tricolour	16ECLOW2P.10/14/10.b1, 12EHLOW4N.10/18/10.b1, 7ECLOW4N.11/25/10.b1, 39EHLOW2N.12/31/10.b2, 39EHLOW2P.12/31/10.b3, 39EHLOW2P.12/31/10.b4, 39EHLOW2P.12/31/10.b5, 39EHLOW2P.12/31/10.b6, 12ECLOW4N.1/01/11.b1, 7ECLOW2P.1/01/11.b2, 7ECLOW4P.1/01/11.b1, 4ECHIGH3P.1/02/11.b1, 7EHLOW2N.1/02/11.b1, 7EHLOW4P.1/02/11.b1, 47ECHIGH3P.1/07/11.b2, 47ECLOW2N.1/07/11.b1, 47ECLOW2N.1/07/11.b2, 47ECLOW2P.1/07/11.b2,

		47ECLOW4N.1/07/11.b1, 47ECLOW4N.1/07/11.b2, 47ECLOW4N.1/07/11.b3, 47ECLOW4N.1/07/11.b4, 47ECLOW4N.1/07/11.b5, 47ECLOW4N.1/07/11.b6, 47ECLOW4P.1/07/11.b3, 47ECLOW4P.1/07/11.b5, 47ECLOW4P.1/07/11.b7, 47EHHIGH1N.1/07/11.b1, 47EHLOW4P.1/07/11.b2, 39EHLOW2P.1/11/11.b4, 39ECLOW2P.1/13/11.b2, 7EHLOW2P.1/19/11.b1, 39ECLOW4P.2/02/11.b2, 12EHLOW4N.2/04/11.b5, 7EHLOW2N.2/05/11.b1, 7EHLOW2P.2/05/11.b1, 47ECLOW4N.2/09/11.b1, 39ECLOW2N.3/10/11.b1, 7EHLOW2P.3/11/11.b1, 47ECHIGH3P.3/13/11.b1, 47ECLOW4P.3/13/11.b2, 39EHLOW2N.5/05/11.b5, 39EHLOW2N.5/05/11.b6, 7EHLOW2N.5/06/11.b1, 7EHLOW2P.5/06/11.b2, 7EHLOW2P.5/06/11.b3, 7EHLOW2P.5/06/11.b5, 7EHLOW2P.5/06/11.b6, 7EHLOW2P.5/06/11.b7, 7EHLOW2P.5/06/11.b8, 16ECHIGH1N.5/10/11.b1, 47ECHIGH3N.5/12/11.b3, 47ECHIGH3N.5/12/11.b4, 47ECLOW4P.5/12/11.b1, 47ECLOW4P.5/12/11.b2, 47EHLOW2P.5/12/11.b1, 47EHLOW4N.5/12/11.b2
	Rogadinae sp.	39EHLOW2P.1/11/11.b2
	Rogadinae white legs, thick antennae	12EHLOW4N.12/31/10.b7, 39ECLOW2N.12/31/10.b2, 39EHHIGH1N.1/11/11.b1, 39EHHIGH1P.1/11/11.b1, 17EHHIGH3P.1/20/11.b1, 47ECLOW4P.1/25/11.b2, 47ECLOW4P.1/25/11.b3, 17ECLOW2N.1/27/11.b2, 17ECLOW2N.2/13/11.b2, 46ECHIGH3P.3/21/11.b2, 46ECLOW4N.3/21/11.b1, 4ECLOW4P.3/23/11.b3, 12ECLOW2N.5/04/11.b1, 39EHLOW2N.5/05/11.b1, 47ECLOW2P.5/12/11.b2, 47ECLOW4N.5/12/11.b1

Table S1.6 Trapped Ichneumonidae morphospecies, and the specimens deposited as vouchers in the New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand. (Underlined highlighted specimens have been deposited instead at the University of Canterbury, Christchurch care of Prof. Jason Tylianakis.)

Subfamily	Morphospecies	Specimens
Campopleginae	*Campoletis* sp. 1	39ECLOW4P.11/17/10.i11, 7EHLOW2P.11/26/10.i1, 47EHHIGH3P.11/27/10.i4, 47ECLOW2P.11/29/10.i1, 12EHLOW4N.12/31/10.i9, 39EHLOW2P.12/31/10.i8, 47EHLOW2P.1/07/11.i2, 39ECLOW4P.1/13/11.i5, 16ECLOW4N.1/17/11.i1, 4EHHIGH3N.1/24/11.i2, 47EHLOW2P.1/25/11.i2, 39EHLOW2P.2/01/11.i5, 12EHLOW4N.2/04/11.i12, 12ECLOW4P.3/08/11.i2, 12EHLOW4N.5/04/11.i3, 39EHLOW2P.5/05/11.i3, 46ECLOW4P.5/08/11.i1, 46EHLOW2P.1/26/11.i4,
	Campoletis sp. 4	12ECLOW4P.1/01/11.i1, 47ECLOW4P.1/07/11.i3, 12ECLOW4P.1/15/11.i2
	Campoplex sp.	47ECLOW2P.10/24/10.i1, 39EHLOW2P.11/16/10.i1, 39ECLOW4P.11/17/10.i12, 39ECLOW4P.11/17/10.i7, 39ECLOW4P.11/17/10.i6, 39ECLOW4P.11/17/10.i9, 39ECLOW4P.11/17/10.i10, 39ECLOW4P.11/17/10.i13, 12EHLOW4N.11/19/10.i7, 16EHLOW2P.11/21/10.i1, 16EHLOW4P.11/21/10.i2 , 17ECLOW4P.11/23/10.i10, 17ECLOW4P.11/23/10.i11, 17ECLOW4P.11/23/10.i2, 17ECLOW4P.11/23/10.i4, 17ECLOW4P.11/23/10.i5, 17ECLOW4P.11/23/10.i7, 17ECLOW4P.11/23/10.i9, 17ECLOW4P.11/23/10.i1, 47EHHIGH3N.11/27/10.i1, 47EHHIGH3N.11/27/10.i3, 47ECLOW2P.11/29/10.i1, 47ECLOW2N.11/29/10.i3, 47ECLOW2N.11/29/10.i4, 46ECHIGH3P.12/02/10.i2, 39ECLOW2N.12/31/10.i1, 39ECLOW4P.12/31/10.i14, 39EHLOW2P.12/31/10.i13, 39EHLOW2P.12/31/10.i15, 39EHLOW2P.12/31/10.i7, 39EHLOW2P.12/31/10.i9, 39ECLOW4P.12/31/10.i9, 39EHLOW2P.12/31/10.i4, 4ECLOW2P.1/02/11.i2, 7EHLOW2P.1/02/11.i1, 4ECLOW4P.1/02/11.i3, 7EHHIGH3P.1/02/11.i2, 17ECLOW4P.1/05/11.i6, 46ECHIGH1P.1/06/11.i1, 47ECLOW4P.1/07/11.i4, 47EHHIGH3P.1/07/11.i7, 47EHLOW2P.1/07/11.i5, 12EHLOW4N.1/10/11.i2, 39ECLOW4P.1/13/11.i2, 39ECLOW4P.1/13/11.i3, 7EHLOW2P.1/19/11.i1, 12EHLOW4N.2/04/11.i10, 12EHLOW4N.2/04/11.i14, 12EHLOW4N.2/04/11.i5, 12EHLOW4N.2/04/11.i13, 47EHHIGH1N.2/08/11.i2, 17ECHIGH1P.2/13/11.i1, 12EHLOW4N.3/06/11.i10, 12EHLOW4N.3/06/11.i2, 12EHLOW4N.3/06/11.i3, 12EHLOW4N.3/06/11.i9, 39EHLOW2P.3/06/11.i4, 12EHLOW4N.3/06/11.i1, 12EHLOW4N.3/06/11.i4, 12EHLOW4N.3/06/11.i5, 12EHLOW4N.3/06/11.i8, 39ECLOW2P.3/10/11.i1, 16EHHIGH3N.3/22/11.i2, 46EHHIGH1P.5/08/11.i1
	Campoplex sp. 13	46ECHIGH1P.12/02/10.i1, 46ECLOW2P.12/02/10.i1, 39ECHIGH1P.12/31/10.i4, 39ECLOW4N.12/31/10.i2, 39ECLOW4P.12/31/10.i10, 39EHHIGH3P.12/31/10.i3, 7ECLOW2P.1/01/11.i4, 4ECLOW2N.1/02/11.i1, 4ECLOW4N.1/02/11.i1, 4ECLOW4N.1/02/11.i5, 4ECLOW4P.1/02/11.i4, 4ECLOW4P.1/02/11.i6, 4ECLOW4P.1/02/11.i7, 16EHHIGH1N.1/03/11.i1, 4EHLOW2P.1/03/11.i3, 17ECHIGH1N.1/05/11.i1, 17ECHIGH1P.1/05/11.i1, 17ECHIGH1P.1/05/11.i2, 17ECLOW4N.1/05/11.i2, 17ECLOW4P.1/05/11.i22, 17EHHIGH3P.1/05/11.i2, 17EHLOW2P.1/05/11.i2, 17EHLOW4N.1/05/11.i1, 17EHLOW4P.1/05/11.i4, 17EHLOW4P.1/05/11.i7, 46ECHIGH1N.1/06/11.i1, 46ECHIGH3N.1/06/11.i1, 46ECLOW4P.1/06/11.i3, 47ECLOW4P.1/07/11.i1, 47ECLOW4P.1/07/11.i6, 47EHHIGH3P.1/07/11.i8, 39EHHIGH3P.1/11/11.i2, 39EHLOW2P.1/11/11.i2, 4EHHIGH3N.1/24/11.i1, 4EHLOW2P.1/24/11.i1, 47ECLOW4P.1/25/11.i2, 47EHLOW2P.1/25/11.i1, 47EHLOW4P.1/25/11.i1, 17ECLOW4P.1/27/11.i13, 17ECLOW4P.1/27/11.i14, 17ECLOW4P.1/27/11.i16, 17ECLOW4P.1/27/11.i19, 17ECLOW4P.1/27/11.i4, 17ECLOW4P.1/27/11.i8, 17ECLOW4P.1/27/11.i9, 39EHLOW2P.2/01/11.i7, 7EHLOW2P.2/05/11.i4, 7EHLOW2P.2/05/11.i5, 47EHHIGH3P.2/08/11.i4, 47EHLOW2N.2/08/11.i1, 47EHLOW4P.2/08/11.i1, 47ECHIGH3P.2/09/11.i1, 47ECHIGH3P.2/09/11.i3, 47ECHIGH3P.2/09/11.i4, 47ECLOW4P.2/09/11.i1, 47ECLOW4P.2/09/11.i4, 17EHHIGH3P.2/12/11.i3, 17EHLOW2P.2/12/11.i1, 4EHHIGH1P.2/15/11.i1, 4EHHIGH3N.2/15/11.i4, 4EHLOW4P.2/15/11.i1, 39ECHIGH3P.3/10/11.i1, 7EHLOW2P.3/11/11.i1, 7EHLOW2P.3/11/11.i2, 47ECLOW4N.3/13/11.i2, 47ECLOW4P.3/13/11.i1, 47EHHIGH3P.3/15/11.i2, 47EHLOW4N.3/15/11.i1, 47EHLOW4P.3/15/11.i1, 17ECLOW4P.5/11/11.i1, 47ECLOW4N.5/12/11.i1
	Campoplex sp. 3	47EHHIGH3P.11/27/10.i5, 4ECLOW4P.1/28/11.i4
	Casinaria sp. 3	39EHLOW2P.2/01/11.i9
	Diadegma brown	39ECLOW4N.10/21/10.i1, 39ECLOW4P.11/17/10.i8, 12EHLOW4N.11/19/10.i9, 12EHLOW4N.12/31/10.i14
	Diadegma gold setae	17ECLOW4P.11/23/10.i13
	Diadegma sp. 1	17EHLOW4P.10/26/10.i2, 12ECLOW2P.11/18/10.i4, 12EHLOW4N.11/19/10.i11, 12EHLOW4N.11/19/10.i13, 12EHLOW4N.11/19/10.i16, 47EHHIGH3N.11/27/10.i4, 47ECLOW2N.11/29/10.i2, 12EHLOW4N.12/31/10.i2, 12EHLOW4N.12/31/10.i26, 39ECLOW4P.12/31/10.i12, 39ECLOW4P.12/31/10.i3, 39ECLOW4P.12/31/10.i4, 39EHLOW2N.12/31/10.i1, 12EHLOW4N.12/31/10.i5, 16EHHIGH3N.1/03/11.i4, 16EHHIGH3P.1/03/11.i3, 17ECLOW4P.1/05/11.i21, 46EHLOW2P.1/06/11.i3, 46EHLOW2P.1/06/11.i4, 12EHLOW4N.1/10/11.i5, 39EHHIGH3P.1/11/11.i1, 39EHLOW2P.1/11/11.i3, 46EHLOW2P.1/26/11.i3, 12EHLOW4N.2/04/11.i4, 12EHLOW4N.2/04/11.i6, 7EHLOW2P.2/05/11.i3, 16ECLOW2P.3/14/11.i1, 16ECLOW2N.5/10/11.i1
	Campoplex black legs	12ECHIGH3P.1/01/11.i2
	NZAC *Campoplex* sp. 10	39ECLOW4P.11/17/10.i2, 39EHHIGH3P.12/31/10.i1, 39EHLOW2P.12/31/10.i6, 12EHLOW4N.12/31/10.i29, 12EHLOW4N.12/31/10.i30, 7EHLOW4N.2/05/11.i2
	NZAC *Campoplex* sp.14 or 18	39ECLOW2P.10/21/10.i1, 17EHLOW4P.10/26/10.i3, 46EHHIGH3P.10/28/10.i2, 46ECLOW4P.10/29/10.i1, 4EHLOW4P.10/31/10.i1, 12EHLOW4N.11/19/10.i10, 16EHHIGH3P.11/21/10.i2, 17ECLOW4N.11/23/10.i1, 47EHLOW2N.11/27/10.i1, 47EHLOW2P.11/27/10.i3, 46ECLOW2P.12/02/10.i2, 12ECLOW2P.1/01/11.i1, 7EHHIGH1N.1/02/11.i2, 16EHLOW2P.1/03/11.i6, 46EHLOW2P.1/26/11.i2, 4ECLOW4P.1/28/11.i3, 4ECLOW2P.1/28/11.i1, 4ECLOW4P.1/28/11.i1, 12ECLOW2P.2/03/11.i2, 7EHLOW2P.2/05/11.i8, 47EHLOW4P.2/08/11.i3, 46ECLOW4N.2/11/11.i1, 4ECLOW4P.2/14/11.i1, 46ECLOW4N.3/21/11.i1, 46ECHIGH3P.3/21/11.i2, 16EHLOW4P.3/22/11.i1, 39EHLOW2P.5/05/11.i4
	NZAC *Campoplex* sp. 16	47EHHIGH3P.11/27/2010.i5
	NZAC *Casinaria* sp. 2	7ECHIGH3N.10/19/10.i1, 39ECLOW2P.10/21/10.i3, 39ECLOW4P.10/21/10.i1, 46ECLOW2P.10/29/10.i1, 12EHLOW4N.11/19/10.i1, 17EHLOW2P.11/24/10.i1,

		7EHHIGH3P.11/26/10.i2, 12EHLOW4N.12/31/10.i12, 39ECHIGH1P.12/31/10.i5, 39EHLOW2P.12/31/10.i3, 12ECLOW4P.1/01/11.i2, 17ECLOW4P.1/05/11.i14, 12EHLOW4N.1/10/11.i4, 16ECLOW2N.1/17/11.i1, 46EHLOW2P.1/26/11.i1, 16ECLOW4P.3/14/11.i1
	Campoplex yellow cox 1,2 v. long T1	17ECLOW4P.11/23/10.i12
Cryptinae	*Xanthocryptus* sp.	16EHHIGH3P.11/21/10.i1, 39ECHIGH1N.12/31/10.i1, 39ECHIGH3P.12/31/10.i2, 39ECHIGH3P.12/31/10.i4, 39ECHIGH3P.12/31/10.i5, 39EHLOW2P.12/31/10.i14, 7ECLOW4N.1/01/11.i1, 16ECLOW2P.1/03/11.i1, 16ECLOW2P.1/03/11.i2, 16EHHIGH3N.1/03/11.i1, 46ECHIGH1P.1/06/11.i3, 46ECHIGH3P.1/06/11.i2, 46EHLOW2P.1/06/11.i2, 46EHLOW2P.1/06/11.i5, 16ECHIGH1P.1/17/11.i1, 7EHHIGH1N.2/05/11.i1, 7EHLOW4N.2/05/11.i1, 16ECHIGH3P.2/06/11.i2, 47ECHIGH3N.2/09/11.i3, 17EHHIGH1N.2/12/11.i2, 12ECHIGH3N.3/08/11.i1, 12ECLOW2P.3/08/11.i1, 39ECHIGH1P.3/10/11.i1, 39ECLOW4P.3/10/11.i1, 39ECLOW4P.3/10/11.i3, 39ECLOW4P.3/10/11.i4, 39ECLOW4P.3/10/11.i5, 46EHHIGH3N.3/20/11.i1
	Xanthocryptus bronze T1	16EHHIGH3P.1/03/11.i4, 39ECHIGH3N.5/05/11.i1
Ctenopelmatinae	*Lathrolestes* sp. 1	4ECLOW4P.1/02/11.i1
	Lathrolestes sp. 1.m	17ECLOW4P.1/05/11.i8
	Lathrolestes sp. 2	16ECLOW2P.2/06/11.i1
	Lathrolestes sp. 2.m	17ECLOW4P.1/05/11.i11, 4ECLOW4P.1/28/11.i2
Ichneumoninae	*Aucklandella* 2 lines	46ECHIGH3P.1/06/11.i1
	Aucklandella black and brown	46ECHIGH3P.1/26/11.i1
	Aucklandella black and brown long ovipositor	47ECLOW2P.11/29/10.i2, 4ECLOW2P.1/02/11.i5
	Aucklandella bright lines.m	12EHLOW4N.12/31/10.i16, 12EHLOW4N.12/31/10.i25, 39ECLOW2P.12/31/10.i2, 47EHLOW4N.1/07/11.i1, 16ECLOW2P.1/17/11.i1, 7EHLOW2P.1/19/11.i2, 7EHLOW2P.1/19/11.i3, 12EHLOW4N.2/04/11.i3, 12EHLOW4N.2/04/11.i2, 47EHHIGH3P.3/15/11.i5, 4EHHIGH1P.3/19/11.i2, 46ECHIGH3P.3/21/11.i1, 16EHLOW4N.3/22/11.i1, 46EHHIGH1P.5/08/11.i2
	Aucklandella bright lines.m v.bigger, black legs	39ECLOW4P.12/31/10.i11, 39ECLOW4P.12/31/10.i15, 39ECLOW4P.12/31/10.i16, 39EHLOW2P.1/11/11.i4, 39ECLOW4P.1/13/11.i1, 39ECLOW4P.1/13/11.i4, 16EHHIGH3P.1/16/11.i3, 39EHLOW2P.2/01/11.i1, 12EHLOW4N.2/04/11.i7, 47ECLOW4N.5/12/11.i2
	Aucklandella colourful.m	12EHLOW4N.10/18/10.i1, 39ECLOW4N.11/17/10.i1, 12ECLOW2N.11/18/10.i3, 12ECLOW2N.11/18/10.i2, 12ECLOW4P.11/18/10.i1, 12ECLOW2P.11/18/10.i3, 12ECLOW4P.11/18/10.i2, 12EHLOW4N.11/19/10.i4, 12EHLOW4N.11/19/10.i5, 16ECLOW2N.11/21/10.i2, 4ECLOW2P.12/01/10.i1, 12EHLOW4N.12/31/10.i23, 12EHLOW4N.12/31/10.i22, 12EHLOW4N.12/31/10.i3, 12EHLOW4N.12/31/10.i24, 4ECLOW4N.1/02/11.i3, 17ECLOW4P.1/05/11.i9, 17ECLOW4P.1/05/11.i2, 47EHLOW2P.1/07/11.i4, 12EHLOW4N.1/10/11.i1, 17ECLOW4P.1/27/11.i6, 17ECLOW4P.1/27/11.i1, 12EHLOW4N.2/04/11.i8
	Aucklandella painted stigma	47ECLOW2N.1/25/11.i1, 17ECLOW2N.1/27/11.i3, 12ECHIGH3P.2/03/11.i1, 47EHLOW4N.2/08/11.i1, 7ECLOW4N.3/12/11.i1, 47EHHIGH3P.3/15/11.i1, 12EHLOW4N.5/04/11.i2
	Aucklandella red	12EHHIGH3N.10/20/10.i1, 12EHHIGH3N.10/20/10.i2, 4ECLOW2P.12/01/10.i2, 46EHHIGH3P.1/06/11.i4, 7EHLOW2P.5/06/11.i2, 4ECLOW2P.5/09/11.i3
	Aucklandella red back large	47ECHIGH1P.11/29/10.i1, 4EHHIGH3P.1/24/11.i1
	Aucklandella red back small	7ECLOW4N.10/19/10.i1, 17ECLOW4P.1/05/11.i16
	Aucklandella red	4EHLOW2N.11/30/10.i1
	Aucklandella shiny red	12EHLOW4N.10/18/10.i2, 39ECHIGH1N.10/21/10.i1, 39ECLOW2P.10/21/10.i5, 46ECLOW2P.10/29/10.i2, 39EHHIGH3N.11/16/10.i1, 39EHHIGH3P.11/16/10.i1, 39EHHIGH3P.11/16/10.i3, 39EHLOW2P.11/16/10.i2, 39EHLOW2P.11/16/10.i4, 39ECHIGH1N.11/17/10.i1, 39ECHIGH3N.11/17/10.i1, 39ECHIGH3P.11/17/10.i1, 39ECLOW2P.11/17/10.i2, 39ECLOW4P.11/17/10.i1, 12EHLOW4N.11/19/10.i12, 12EHLOW4P.11/19/10.i1, 16EHLOW4P.11/21/10.i3, 47EHLOW2P.11/27/10.i2, 47ECLOW4N.11/29/10.i1, 47ECLOW2N.11/29/10.i1, 39ECHIGH1N.12/31/10.i3, 12ECLOW4P.1/15/11.i3, 39EHLOW2P.2/01/11.i3, 47ECLOW2P.2/09/11.i1, 39ECHIGH1N.3/10/11.i1, 47ECLOW2N.5/12/11.i1
	Aucklandella slim brown.m	39ECHIGH3P.12/31/10.i6, 39ECLOW4P.12/31/10.i2, 4ECLOW4P.1/02/11.i5, 46ECHIGH1P.1/06/11.i2, 39ECLOW4P.1/13/11.i6, 17ECHIGH3P.1/27/11.i1, 17ECHIGH3P.1/27/11.i2, 17ECLOW4P.1/27/11.i2, 47ECLOW4P.2/09/11.i2, 47ECLOW4P.2/09/11.i3, 17EHHIGH1N.2/12/11.i1, 17ECHIGH1P.2/13/11.i2, 47ECLOW4P.3/13/11.i4
	Aucklandella small sp.m	17ECLOW2N.1/27/11.i2
	Aucklandella technicolor	12EHLOW4N.12/31/10.i19, 17EHLOW4N.10/26/10.i1, 46ECLOW2P.10/29/10.i3, 4EHHIGH3P.10/31/10.i1, 39ECLOW2N.11/17/10.i3, 12EHLOW4N.11/19/10.i17, 17ECLOW4P.11/23/10.i8, 7EHLOW2N.11/26/10.i1, 46ECLOW2P.12/02/10.i3, 46ECLOW4P.12/02/10.i1, 4ECLOW2P.1/02/11.i3, 16EHHIGH1P.1/03/11.i1, 17EHHIGH3N.1/05/11.i1, 17EHLOW4P.1/05/11.i3, 47EHLOW4P.1/07/11.i2, 7EHHIGH3P.1/19/11.i1, 7EHLOW2P.1/19/11.i4, 17EHLOW2N.1/20/11.i2, 4EHLOW2N.1/24/11.i1, 4ECLOW2P.1/28/11.i2, 7EHLOW2P.2/05/11.i2, 47EHHIGH1N.2/08/11.i1, 17EHLOW2N.2/12/11.i1, 17EHLOW2N.2/12/11.i1, 17EHLOW4N.2/12/11.i1, 4ECLOW2P.2/14/11.i1, 39EHHIGH1P.3/06/11.i2, 7EHHIGH1P.3/11/11.i1, 7EHLOW2P.3/11/11.i3, 17EHHIGH3N.3/18/11.i4, 17EHHIGH3N.3/18/11.i1, 17EHHIGH3N.3/18/11.i2, 17EHHIGH3N.3/18/11.i5, 46ECLOW2P.3/21/11.i1, 46ECLOW2P.3/21/11.i2, 12EHLOW4N.5/04/11.i4, 4ECHIGH1P.5/09/11.i1, 17ECLOW2N.5/11/11.i1, 17ECLOW4P.5/11/11.i4
	Aucklandella thick antennae yellow	39EHHIGH3P.11/16/10.i4, 12ECLOW2P.11/18/10.i2, 12EHLOW4N.11/19/10.i6, 17EHHIGH3P.11/24/10.i2, 7ECLOW2P.11/25/10.i1, 47EHLOW4P.11/27/10.i3, 12EHLOW4N.12/31/10.i6, 12EHLOW4N.12/31/10.i10, 12EHLOW4N.12/31/10.i17, 12EHLOW4N.12/31/10.i18, 4ECHIGH1P.1/02/11.i2, 16EHLOW2P.1/03/11.i5, 17ECLOW4P.1/05/11.i19, 17ECLOW4P.1/05/11.i7, 17ECLOW2P.1/05/11.i2, 4ECHIGH1P.1/28/11.i1, 17EHHIGH3P.2/12/11.i1, 17ECLOW2N.3/17/11.i1, 39ECLOW2P.5/05/11.i1, 39EHHIGH1P.5/05/11.i2, 46EHHIGH1N.5/08/11.i1, 4ECHIGH3P.5/09/11.i1, 16ECHIGH1P.5/10/11.i2, 17EHLOW4N.5/11/11.i2, 47ECLOW2P.5/12/11.i1
	Aucklandella thick ovipositor	17EHHIGH1P.11/24/10.i3
	Aucklandella yellow stripes	46ECLOW4P.1/06/11.i2
	Degithina 3 spots	12EHLOW4N.12/31/10.i31, 4EHLOW4P.1/03/11.i2, 4EHLOW2N.1/03/11.i1, 4EHLOW4P.1/03/11.i1, 17ECLOW4P.1/05/11.i15, 17EHLOW4N.1/05/11.i3, 12EHLOW4N.1/10/11.i7, 12EHHIGH3N.1/10/11.i1, 12EHLOW4N.1/10/11.i6, 47ECLOW2P.1/25/11.i1, 4EHLOW2P.2/15/11.i1

	Ichneumon bronze 3 lateral spots.m	47EHHIGH3P.2/08/11.i5
	Ichneumon no spot black tail	12ECLOW2P.1/01/11.i3, 17ECLOW4P.2/13/11.i6
	Ichneumon one spot black tail.m	39ECLOW2N.12/31/10.i3, 39ECLOW4P.12/31/10.i1, 39ECLOW4P.12/31/10.i8, 39ECLOW4P.2/02/11.i1, 7EHLOW2N.3/11/11.i1
	Ichneumon one spot bronze.m	12EHLOW4N.2/04/11.i1, 12EHLOW4N.2/04/11.i17
	Ichneumon one spot brown tail.m	39ECHIGH1P.12/31/10.i8, 39ECLOW4N.12/31/10.i6, 39ECLOW4P.12/31/10.i18, 39EHLOW2P.12/31/10.i19, 39ECLOW4P.1/13/11.i7, 7EHLOW2P.2/05/11.i6, 39ECLOW4P.3/10/11.i6
	Ichneumon small 1 spot black tail.m	46EHLOW2P.1/26/11.i5
	Ichneumon small 1 spot black tail	39ECLOW4P.2/02/11.i2, 47EHLOW4P.2/08/11.i2
Mesochorinae	*Mesochorus* sp.1	39ECLOW2P.10/21/10.i6, 39ECLOW2P.11/17/10.i1, 39ECLOW2P.11/17/10.i4, 12ECLOW2N.11/18/10.i1, 47EHHIGH3P.11/27/10.i2, 47EHHIGH3P.11/27/10.i1, 12EHHIGH1N.12/31/10.i1, 39ECLOW4N.12/31/10.i1, 7EHHIGH1P.1/02/11.i1, 47ECHIGH3P.1/07/11.i2, 47ECHIGH3P.1/07/11.i3, 47ECLOW4P.1/07/11.i5, 47EHHIGH3N.1/07/11.i1, 47EHHIGH3P.1/07/11.i3, 47EHHIGH3P.1/07/11.i5, 39EHHIGH3P.1/11/11.i3, 39EHLOW2P.1/11/11.i1, 7ECHIGH1P.1/21/11.i1, 47ECHIGH3P.1/25/11.i1, 47EHHIGH3P.1/25/11.i3, 39EHLOW2N.2/01/11.i1, 39EHLOW2P.2/01/11.i2, 39EHLOW4P.2/01/11.i1, 47EHHIGH3P.2/08/11.i2, 47EHHIGH3P.2/08/11.i3, 47ECHIGH3P.2/09/11.i2, 47ECHIGH3P.2/09/11.i5, 47ECLOW4N.2/09/11.i2, 39EHLOW2P.3/06/11.i1, 39EHLOW2P.3/06/11.i3, 7EHHIGH1N.3/11/11.i1, 7ECHIGH3P.3/12/11.i1, 47ECHIGH3P.3/13/11.i1, 16ECHIGH1N.3/14/11.i2, 47EHHIGH3P.3/15/11.i3, 47EHHIGH3P.3/15/11.i4, 4EHHIGH1N.3/19/11.i1, 46ECLOW2P.3/21/11.i4, 39EHHIGH3N.5/05/11.i1, 7ECHIGH3N.5/06/11.i1
	Mesochorus sp.2	47ECLOW4P.5/12/11.i2, 16EHLOW2N.5/13/11.i1
	Mesochorus sp.3	4ECLOW4N.1/28/11.i1
Metopiinae	*Carria* sp.	17EHLOW2P.1/05/11.i1
Ophioninae	*Ophion* sp. 1	39EHHIGH3P.12/31/10.i2
Orthocentrinae	*Megastylus* sp. 1	39ECLOW2P.10/21/10.i2, 12EHLOW4N.11/19/10.i14, 12EHLOW4N.11/19/10.i8, 12EHLOW4N.12/31/10.i1, 12EHLOW4N.12/31/10.i27, 12EHLOW4N.12/31/10.i7, 39ECLOW4P.12/31/10.i5, 39ECLOW4P.12/31/10.i6, 39EHLOW2P.12/31/10.i10, 39ECLOW4N.12/31/10.i3, 4ECLOW4N.1/02/11.i2, 4ECLOW4P.1/02/11.i2, 17ECLOW4P.1/05/11.i12, 17ECLOW4P.1/05/11.i13, 47ECLOW4P.1/07/11.i2, 47EHHIGH3P.1/07/11.i1, 47EHLOW4P.1/07/11.i1, 47ECLOW2P.1/07/11.i1, 12EHLOW4N.1/10/11.i3, 17ECLOW4N.1/27/11.i2, 17ECLOW4P.1/27/11.i3, 17ECLOW4P.1/27/11.i5, 39EHLOW2N.2/01/11.i3, 12ECLOW2N.2/03/11.i1, 17ECLOW4P.2/13/11.i2, 17ECLOW4P.2/13/11.i4, 17ECLOW4P.2/13/11.i5, 17ECLOW4P.2/13/11.i7, 17ECLOW4P.2/13/11.i9, 4EHLOW4N.2/15/11.i1, 12EHLOW4N.3/06/11.i6, 47EHLOW4P.3/15/11.i2, 12ECLOW4P.5/04/11.i1, 39EHLOW2P.5/05/11.i1, 4ECLOW2P.5/09/11.i1, 16ECLOW2P.5/10/11.i1, 4EHLOW2P.5/10/11.i1, 17ECHIGH1P.5/11/11.i1, 17ECLOW4P.5/11/11.i2
	Megastylus sp. 2	39ECLOW2N.11/17/10.i1, 39ECLOW2N.11/17/10.i2, 39ECLOW2N.11/17/10.i4, 39EHLOW2P.12/31/10.i16, 39EHLOW2P.12/31/10.i2, 46ECLOW4P.1/26/11.i1, 16ECLOW4N.2/06/11.i1, 39EHLOW2N.3/06/11.i3, 39EHLOW2N.3/06/11.i1, 39ECLOW4P.3/10/11.i2, 7EHLOW4P.3/11/11.i1, 46ECLOW2P.3/21/11.i3, 39EHLOW2N.5/05/11.i1, 7ECLOW2P.5/06/11.i1, 46ECLOW2P.5/08/11.i1, 16ECLOW2P.5/10/11.i2, 17ECLOW2P.5/11/11.i1
	"Gelis wings"	4ECLOW2P.12/01/10.i3, 46ECHIGH1P.12/02/10.i2, 46ECHIGH3P.12/02/10.i1, 46EHHIGH3P.12/02/10.i2, 46EHHIGH3P.12/02/10.i1, 12EHHIGH1P.12/31/10.i1, 12EHLOW2P.12/31/10.i1, 39EHHIGH3P.12/31/10.i4, 12ECHIGH1N.1/01/11.i1, 12ECHIGH3N.1/01/11.i1, 12ECHIGH3P.1/01/11.i4, 7ECLOW2P.1/01/11.i1, 4ECHIGH1P.1/02/11.i1, 4ECHIGH1P.1/02/11.i3, 7EHHIGH1N.1/02/11.i1, 4ECLOW2P.1/02/11.i1, 16EHHIGH3P.1/03/11.i2, 16EHLOW2N.1/03/11.i2, 16EHLOW2P.1/03/11.i4, 4EHHIGH1P.1/03/11.i1, 4EHLOW4N.1/03/11.i1, 46EHHIGH3P.1/06/11.i3, 46EHLOW2P.1/06/11.i1, 7ECLOW2P.1/21/11.i2, 4ECLOW4P.1/28/11.i5, 12EHHIGH3N.2/04/11.i1, 16ECHIGH3P.2/06/11.i1, 16EHHIGH3N.2/06/11.i1, 47ECHIGH3N.2/09/11.i2, 7ECLOW2P.2/09/11.i1, 7ECLOW4P.2/09/11.i1, 46EHHIGH3P.2/11/11.i1, 4EHHIGH3N.2/15/11.i1, 4EHHIGH3N.2/15/11.i2, 4EHHIGH3P.2/15/11.i1, 4EHLOW4P.2/15/11.i2, 39EHHIGH3P.3/06/11.i1, 7ECLOW2P.3/12/11.i1, 4EHHIGH1P.3/19/11.i1, 4EHHIGH1P.3/19/11.i3, 4EHHIGH1P.3/19/11.i4, 46EHHIGH3P.3/20/11.i1, 4ECHIGH1P.3/23/11.i1
	Aclastus all tan.m	39EHLOW2P.2/01/11.i8
	Aclastus bright yellow face.m	47EHHIGH3N.11/27/10.i2
	Aclastus red	17ECLOW4P.1/05/11.i1, 47ECLOW4P.3/13/11.i3
	Aclastus white legs	17EHHIGH1P.11/24/10.i2, 4EHLOW2P.1/03/11.i1, 17ECLOW4P.1/05/11.i10
	Aclastus yellow face	17ECLOW4P.2/13/11.i8
	Aclosmation black, orange abdomen	12ECHIGH3N.11/18/10.i1, 12EHHIGH3P.12/31/10.i2, 12EHLOW4P.12/31/10.i1, 16EHLOW2N.1/03/11.i1, 16EHLOW4N.1/03/11.i1, 17ECLOW2N.1/05/11.i1, 17ECLOW2P.1/05/11.i1, 17ECLOW2P.1/05/11.i3, 17ECLOW2P.1/05/11.i4, 46EHHIGH3P.1/06/11.i2
	Aclosmation black, orange abdomen.m	17ECLOW4N.1/05/11.i3, 17ECLOW4P.1/05/11.i3, 17ECLOW4P.1/05/11.i17, 47EHLOW2P.1/07/11.i3, 47EHLOW4P.1/07/11.i4, 17ECLOW4P.1/27/11.i7
	Aclosmation black, yellow legs	12EHLOW4N.12/31/10.i11, 12EHLOW4N.12/31/10.i21, 16EHHIGH3P.2/06/11.i2
	Aclosmation black, yellow legs.m	39ECLOW4P.11/17/10.i4, 16ECLOW2N.11/21/10.i1, 12EHLOW4N.12/31/10.i28
	Aclosmation brown gaster	16EHHIGH3N.1/03/11.i3, 16EHHIGH3P.1/03/11.i1
	Aclosmation downward ovipositor	4ECLOW2P.1/02/11.i4
	Aclosmation small, black cox 3.m	17EHLOW4N.5/11/11.i1
	Aclosmation tiny shiny.m	39ECLOW2P.10/21/10.i4, 46EHHIGH3P.10/28/10.i1, 46ECLOW2N.10/29/10.i1, 47ECHIGH3P.1/25/11.i2, 46ECLOW4P.1/26/11.i2, 17ECLOW4N.1/27/11.i1, 39ECHIGH3P.2/02/11.i2, 12EHLOW4N.2/04/11.i15, 12EHLOW4N.2/04/11.i16, 17EHLOW4P.2/12/11.i1, 17ECHIGH1N.2/13/11.i1, 12ECLOW4N.3/08/11.i1, 4EHLOW4P.5/10/11.i3
	Anacis banded	47ECLOW2N.10/24/10.i2, 47ECLOW2N.1/07/11.i1, 47EHLOW4P.1/07/11.i3, 7ECLOW4N.3/12/11.i2, 47ECLOW4P.3/13/11.i2, 4EHHIGH1P.3/19/11.i1, 4EHLOW2P.3/19/11.i1, 4EHLOW2P.3/19/11.i2, 16ECLOW4P.5/10/11.i1
	Anacis brown flank, banded.m	7EHLOW4N.11/26/10.i1, 7ECLOW4P.1/21/11.i1, 46EHLOW2N.3/20/11.i1, 12ECLOW4N.5/04/11.i1, 47ECLOW2P.5/12/11.i3

Anacis close to nr. Amblyaclastus	17ECLOW4P.1/05/11.i4
Anacis ordinary black, brown legs.m	7EHLOW4P.1/19/11.i1
Anacis sp.2	12ECHIGH3P.1/01/11.i3
Anacis sp.3	12EHLOW4N.11/19/10.i2
Anacis white coxae	39ECHIGH1N.12/31/10.i2, 46EHHIGH1P.1/06/11.i1, 7ECLOW2P.1/21/11.i3, 4EHLOW4P.5/10/11.i2
Genus *Allophroides* dark stigma	47ECLOW4N.10/24/10.i1, 47EHHIGH3P.11/27/10.i3, 47EHLOW2P.11/27/10.i1, 47EHLOW4P.11/27/10.i4, 12ECLOW2N.1/01/11.i1, 39EHHIGH3P.1/11/11.i4
Genus *Allophroides* light stigma.m	4ECLOW2P.5/09/11.i4
Genus B/G shiny brown	39EHHIGH3P.2/01/11.i1
Genus B shiny brown, black tail	16ECLOW2N.2/06/11.i1, 47EHHIGH3P.2/08/11.i1, 39EHLOW2N.3/06/11.i2, 39EHLOW2P.3/06/11.i2, 16ECLOW2P.3/14/11.i2, 47EHHIGH3P.5/12/11.i1
Genus B sp.1.m	39ECLOW4N.1/13/11.i1
Genus B sp.2.m	16ECLOW4P.1/03/11.i1, 47EHHIGH3P.1/07/11.i4, 47EHHIGH3P.1/25/11.i1, 47EHHIGH3P.1/25/11.i2
Genus B yellow drop	39EHLOW2P.11/16/10.i3, 16ECHIGH3N.11/21/10.i1, 39EHHIGH1P.12/31/10.i1, 39EHLOW2P.12/31/10.i11, 46ECLOW2N.1/06/11.i1, 39EHHIGH1P.3/06/11.i3, 39EHHIGH1P.5/05/11.i1, 39EHHIGH1P.5/05/11.i3, 39EHLOW2P.5/05/11.i2, 4ECLOW2P.5/09/11.i2, 16ECHIGH1P.5/10/11.i1
Genus B yellow drop.m	7EHHIGH3P.1/02/11.i1
Genus B nr. yellow drop	16ECHIGH3P.1/03/11.i2
Genus G short face, shiny black	17EHLOW4P.5/11/11.i1
Genus G/K braconid-looking.m	39EHLOW2P.11/16/10.i7
Genus G/K small brown and yellow	12ECLOW2P.10/16/10.i1, 17EHLOW4P.10/26/10.i1, 39EHLOW2N.11/16/10.i1, 17EHHIGH1N.11/24/10.i2, 17EHHIGH3P.11/24/10.i1, 17EHLOW2N.11/24/10.i1, 17EHLOW2N.11/24/10.i2, 17EHLOW2P.11/24/10.i3, 17EHLOW4N.11/24/10.i1, 17EHLOW4N.11/24/10.i3, 17EHLOW4P.11/24/10.i2, 17EHLOW4P.11/24/10.i3, 17EHLOW4P.11/24/10.i4, 7EHLOW4N.11/26/10.i2, 17EHHIGH3P.1/05/11.i1, 17EHLOW4P.1/05/11.i5
Genus G/K tiny, droplet gaster	39EHLOW2N.10/20/10.i1, 39EHLOW2N.10/20/10.i2
Genus G red brown, droplet gaster	39ECLOW4P.12/31/10.i17, 39EHLOW2P.3/06/11.i6, 12ECLOW4P.3/08/11.i1
Genus G short face, shiny black	12EHLOW4N.12/31/10.i4, 7ECLOW2P.1/01/11.i6, 17EHLOW4N.1/05/11.i2, 17EHLOW4P.1/05/11.i1, 39EHLOW2P.1/11/11.i7, 12EHLOW4N.2/04/11.i9, 46ECLOW4P.2/11/11.i1, 17EHHIGH3N.2/12/11.i1, 17EHHIGH3P.2/12/11.i2, 17EHLOW4P.2/12/11.i2, 17EHLOW4P.2/12/11.i3, 39EHLOW2P.5/05/11.i6, 7EHLOW2P.5/06/11.i4, 17EHHIGH3P.5/11/11.i1, 17EHLOW4N.5/11/11.i3, 17EHLOW2N.5/11/11.i1
Genus K/Ao large cell	39EHLOW2P.11/16/10.i5, 39ECLOW4P.11/17/10.i3, 39ECLOW4P.11/17/10.i5, 17EHHIGH1N.11/24/10.i1, 39EHLOW2P.12/31/10.i20, 39EHLOW2P.12/31/10.i22, 39EHLOW2P.12/31/10.i5, 46EHHIGH1N.1/06/11.i1, 39EHLOW2P.1/11/11.i6, 39ECLOW4P.1/13/11.b1, 17ECLOW4P.1/27/11.i12, 39EHLOW2P.2/01/11.i4, 39EHLOW2P.2/01/11.i6, 39EHHIGH3P.3/06/11.i3, 39EHLOW2N.3/06/11.i1, 39EHLOW2N.3/06/11.i2, 39EHLOW2P.3/06/11.i10, 39ECLOW4P.3/10/11.i7, 4EHLOW2P.5/10/11.i2, 4EHLOW2P.5/10/11.i5
Habronyx sp. 1.m	39EHHIGH3P.11/16/10.i2, 17ECLOW4P.11/23/10.i3, 12EHLOW2P.12/31/10.i2
nr. *Amblyaclastus* sp. 1	47ECHIGH3P.10/24/10.i1, 47ECLOW2N.10/24/10.i1, 17EHHIGH1N.10/26/10.i1, 17ECHIGH1P.10/27/10.i1, 4EHHIGH1P.10/31/10.i1, 39ECLOW2P.11/17/10.i3, 12ECLOW2P.11/18/10.i1, 12ECLOW4P.11/18/10.i3, 12ECLOW4P.11/18/10.i4, 12EHHIGH3N.11/19/10.i1, 16EHLOW4P.11/21/10.i1, 17EHHIGH1P.11/24/10.i1, 17EHLOW2P.11/24/10.i2, 17EHLOW4N.11/24/10.i2, 17EHLOW4P.11/24/10.i1, 7ECHIGH3P.11/25/10.i1, 47EHHIGH1P.11/27/10.i2, 47EHLOW4P.11/27/10.i1, 47ECLOW2N.11/29/10.i5, 47ECLOW2P.11/29/10.i2, 4EHLOW2P.11/30/10.i1, 46ECHIGH3P.12/02/10.i3, 39ECLOW4N.12/31/10.i5, 39ECLOW4P.12/31/10.i13, 39EHLOW2P.12/31/10.i1, 12EHHIGH3P.12/31/10.i1, 39ECHIGH1P.12/31/10.i6, 39ECLOW4N.12/31/10.i7, 39EHHIGH1N.12/31/10.i1, 39ECHIGH1P.12/31/10.i2, 12ECLOW2N.1/01/11.i2, 12ECLOW2N.1/01/11.i3, 12ECLOW4P.1/01/11.i3, 7ECLOW2P.1/01/11.i3, 7ECLOW2P.1/01/11.i5, 12ECHIGH3P.1/01/11.i1, 4EHLOW2P.1/03/11.i2, 17ECLOW4N.1/05/11.i1, 46EHHIGH3P.1/06/11.i1, 47EHLOW2P.1/07/11.i6, 47ECHIGH3P.1/07/11.i1, 7ECLOW2P.1/21/11.i1, 4EHLOW4P.1/24/11.i1, 17ECLOW2N.1/27/11.i1, 17ECLOW4P.1/27/11.i11, 17ECLOW4P.1/27/11.i17, 39ECHIGH3N.2/02/11.i1, 12ECLOW2P.2/03/11.i1, 12ECLOW4N.2/03/11.i1, 7EHLOW2P.2/05/11.i7, 17ECLOW2N.2/13/11.i1, 17ECLOW4P.2/13/11.i1, 17ECLOW4P.2/13/11.i3, 4ECHIGH3N.2/14/11.i1, 4EHHIGH3N.2/15/11.i3, 39EHHIGH1N.3/06/11.i1, 39EHLOW2P.3/06/11.i9, 12ECLOW4N.3/08/11.i3, 7EHLOW2N.3/11/11.i2, 47ECLOW4N.3/13/11.i1, 47EHHIGH3N.3/15/11.i1, 47EHLOW2N.3/15/11.i1, 47EHLOW2P.3/15/11.i1, 17ECLOW4P.3/17/11.i2, 17EHLOW2N.3/18/11.b3, 4EHLOW4N.3/19/11.i1, 4EHHIGH1N.3/19/11.i2, 4ECLOW2N.3/23/11.i1, 12EHLOW4N.5/04/11.i1, 12EHLOW4N.5/04/11.i5, 12EHLOW4N.5/04/11.i6, 12EHLOW4N.5/04/11.i7, 39EHHIGH1N.5/05/11.i1, 39EHLOW2P.5/05/11.i5, 39EHHIGH1P.5/05/11.i4, 7EHLOW2P.5/06/11.i1, 46EHHIGH3P.5/08/11.i1, 4ECHIGH1P.5/09/11.i3, 4ECHIGH3P.5/09/11.i2, 4ECLOW4P.5/09/11.i1, 16ECLOW2P.5/10/11.b11, 16ECLOW4N.5/10/11.i1, 4EHHIGH3P.5/10/11.i1, 4EHHIGH3P.5/10/11.i2, 4EHHIGH3P.5/10/11.i3, 4EHLOW2N.5/10/11.i1, 4EHLOW2N.5/10/11.i3, 4EHLOW2P.5/10/11.i3, 4EHLOW4P.5/10/11.i4, 4EHLOW4P.5/10/11.i5, 4EHLOW2N.5/10/11.i2, 4EHLOW2P.5/10/11.i4, 4EHLOW4P.5/10/11.i1, 4EHHIGH3N.5/10/11.i1, 17EHHIGH3N.5/11/11.i1, 47ECLOW2P.5/12/11.i2, 47ECLOW4P.5/12/11.i1, 47EHLOW2N.5/12/11.i1, 47ECLOW2P.5/12/11.i4
nr. *Amblyaclastus* sp. 1.m	7ECHIGH3N.1/01/11.i1, 4ECLOW2P.3/23/11.i1, 4EHLOW4N.5/10/11.i1
nr. *Amblyaclastus* sp. 2	39ECHIGH3P.12/31/10.i1, 12EHLOW4N.12/31/10.i15, 12EHLOW4N.12/31/10.i20, 39ECLOW2N.12/31/10.i2, 39EHHIGH1P.12/31/10.i2, 39EHLOW2P.12/31/10.i17, 39ECHIGH3P.12/31/10.i3, 16ECLOW4P.1/03/11.i2, 16EHLOW2P.1/03/11.i3, 16EHHIGH3N.1/03/11.i2, 17ECLOW4N.1/05/11.i4, 17EHLOW4P.1/05/11.i2, 17EHLOW2N.1/05/11.i1, 17EHLOW2N.1/05/11.i2, 17EHLOW2P.1/05/11.i3, 7EHLOW2N.1/19/11.i1, 17ECLOW4P.1/27/11.i15, 17ECLOW4P.1/27/11.i18, 39EHLOW2N.2/01/11.i2, 7EHLOW2P.2/05/11.i1, 39EHHIGH1P.3/06/11.i1, 39EHLOW2P.3/06/11.i7, 39ECLOW2P.3/10/11.i2, 17ECLOW4P.3/17/11.i1
nr. *Amblyaclastus* sp. 2.m	16EHLOW2P.11/21/10.i2, 16EHHIGH3P.11/21/10.i3, 12EHHIGH3N.12/31/10.i1, 7ECLOW2P.1/01/11.i2
nr. *Amblyaclastus* sp. 3	17EHLOW2N.1/05/11.i3, 46ECLOW4P.1/06/11.i1

	nr. *Amblyaclastus* sp. 3.m	16EHHIGH3N.3/22/11.i3
	nr. *Amblyaclastus* sp. 4	47ECLOW2N.10/24/10.i3, 39EHLOW2P.12/31/10.i12, 12EHLOW4N.2/04/11.i11, 16ECLOW2P.3/14/11.i1, 17EHHIGH3N.3/18/11.i3, 17EHLOW4P.3/18/11.i1
	nr. *Amblyaclastus* sp. 4.m	12EHLOW4N.11/19/10.i3, 39ECLOW2P.12/31/10.i1, 39ECLOW4P.12/31/10.i7, 12EHLOW4N.12/31/10.i8, 46EHHIGH3P.1/06/11.i5, 39EHLOW2P.3/06/11.i8
	nr. *Amblyaclastus* sp. 5m	12EHLOW4N.11/19/10.i15
	nr. *Amblyaclastus* sp. 6.m	47ECLOW4N.2/09/11.i1, 12ECLOW4P.3/08/11.i3, 17ECLOW4P.5/11/11.i3
	nr. *Glabridorsum* sp. 1	17ECLOW4P.10/27/10.i1
	nr. *Glabridorsum* sp. 1.m	17ECLOW4P.10/27/10.i2, 17ECLOW4P.10/27/10.i3, 17ECLOW4P.10/27/10.i4, 17ECLOW4P.10/27/10.i5, 17ECLOW4P.10/27/10.i6, 17ECLOW4P.11/23/10.i6, 4EHLOW4P.11/30/10.i1, 7EHLOW4P.1/02/11.i1, 17ECLOW4P.1/05/11.i20, 47EHHIGH3P.1/07/11.i2
	Zealochus brown/orange.m	39ECLOW4N.12/31/10.i4
	Zealochus ordinary black, yellow legs	39EHLOW2P.11/16/10.i8
	Zealochus ordinary black, yellow legs.m	39EHLOW2N.10/20/10.i3, 39EHLOW2P.12/31/10.i21
	Neorhacodes or *Hybrizon*?	47ECLOW2N.11/29/10.i6

Appendix 2

A.2.1 Supplementary tables and figures for Chapter 2

Figure S2.1. Bi-directional malaise-type insect flight trap. Insects flying out of plantation forest and out of native forest were collected in separate jars.

Table S2.1. Coefficients from the best-fitting GLMM with binomial error to determine whether incidence of broken traps was related to herbivore reduction treatment, forest type, collection, trap height, or any interactions with herbivore reduction treatment. Forest type within site within block were included as random factors. Collection was the only predictor retained in the final model. Collection 6 is used as the intercept condition in order to display contrasts for collection dates with the most widely-varying estimates. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (collection 6)	-3.1529	0.4718	-6.68	**<0.0001**
Collection 2	-0.3192	0.5826	-0.55	0.584
Collection 3	-0.1493	0.5596	-0.27	0.790
Collection 4	-17.8588	2640	-0.01	0.995
Collection 5	-0.3192	0.5826	-0.55	0.584
Collection 7	-17.8852	2680	-0.01	0.995

Table S2.2. Coefficients of a GLMM with Poisson errors in which caterpillar number was predicted by herbivore reduction treatment (herbivore reduction vs. control), forest type (plantation vs. native), collection (immediately before herbivore reduction vs. immediately after herbivore reduction), and their interactions, with forest type nested within site, nested within block as random effects. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (Before, Native, Control)	3.1824	0.2830	11.24	**<0.0001**
Treatment (Herbivore reduction)	0.4014	0.3958	1.01	0.3104
Forest (Plantation)	-0.6504	0.3874	-1.68	0.0931
Collection (After)	0.3467	0.3764	0.92	0.3570
Treatment*Forest (Herbivore reduction, Plantation)	0.7411	0.5378	1.38	0.1683
Treatment*Collection (Herbivore reduction, After)	-0.1999	0.5289	-0.38	0.7055
Forest*Collection (Plantation, After)	0.3507	0.5389	0.65	0.5152
Treatment*Forest*Collection (Herbivore reduction, Plantation, After)	-2.1043	0.7622	-2.76	**0.0058**

Table S2.3. Coefficients from the best-fitting GLMM with Poisson errors testing whether forest type predicted the abundance of generalist predators in flight traps at control edges was between plantation and native forest over all collections. Sampling effort was included as a fixed effect in the full model, and site was included as a random factor. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (From Native)	1.7278	0.5762	3.00	**0.0027**
Forest (From Plantation)	1.7865	0.3096	5.77	**< 0.0001**

Table S2.4. Coefficients from the best-fitting GLMM with Poisson errors testing whether forest type predicted the abundance of parasitoids in flight traps at control edges between plantation and native forest over all collections. Sampling effort was included as a fixed effect, and site was included as a random factor. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (From Native)	5.9660	1.3997	4.26	< **0.0001**
Forest (From Plantation)	0.6514	0.1549	4.20	< **0.0001**
Sampling Effort	-0.3884	0.2207	-1.76	0.0784

Table S2.5. Coefficients from the best-fitting GLMM with Poisson errors testing whether herbivore reduction treatment, forest type, or their interaction predicted the abundance of generalist predators in flight traps after the treatment. Sampling effort was included as a fixed effect, and forest type, within site, within block were included as random factors. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (Control, From Native)	3.9287	2.6322	1.49	0.136
Treatment (Herbivore reduction)	1.1775	0.7663	1.54	0.124
Forest (From Plantation)	1.6762	0.2325	7.21	< **0.0001**
Sampling effort	-2.8406	1.8021	-1.58	0.115
Treatment*Forest (Herbivore reduction, From Plantation)	-1.7413	0.3181	-5.47	< **0.0001**

Table S2.6. Coefficients from the best-fitting GLMM with Poisson errors testing whether herbivore reduction treatment, collection, forest type, and their interactions predicted the abundance of parasitoids in flight traps. Sampling effort was included as a fixed predictor and forest type, within site, within block were included as random factors. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (From Native, Before)	4.6244	0.8875	5.21	< **0.0001**
Forest (From Plantation)	0.7846	0.1868	4.20	< **0.0001**
Collection (After)	-1.5486	0.4485	-3.45	**0.0006**
Sampling Effort	-0.8033	0.3174	-2.53	**0.0114**

Table S2.7. Coefficients from the best-fitting GLMM with Poisson errors testing whether the abundance of parasitoids in flight traps was predicted by forest type, herbivore reduction treatment, collection, or any interactions between these variables, including only reared species known to parasitize Lepidoptera at these sites. Sampling effort was included as a fixed predictor, and forest type, nested within site, nested within block were included as random factors. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (From Native, Before)	1.0739	0.2503	4.29	<**0.0001**
Forest (From Plantation)	0.9201	0.2646	3.48	**0.0005**
Collection (After)	-0.5962	0.1144	-5.21	<**0.0001**

Table S2.8. Coefficients from the best-fitting GLMM with binomial errors testing whether parasitism rates in native forest were predicted by herbivore reduction treatment in the adjacent plantation forest, collection, or their interaction. Site nested within block were included as random factors. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (Before)	-2.3504	0.2226	-10.56	< **0.0001**
Collection (After)	0.6908	0.1536	4.498	< **0.0001**

Table S2.9. Coefficients from the best-fitting GLMM with Poisson errors testing whether parasitism events in native forest were predicted by herbivore reduction treatment in the adjacent plantation forest, collection, or their interaction. Site nested within block were included as random factors. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (Before)	0.1772	0.2503	0.71	0.4790
Collection (After)	1.1109	0.2359	4.71	**< 0.0001**

Table S2.10. Coefficients from the best-fitting GLMM with binomial errors testing whether herbivore reduction treatment, or collection could predict parasitism rate in native forest, with hosts parasitized by non-ichneumonid or braconid parasitoids excluded from parasitism rate calculations. Forest type, nested within site, nested within block were included as random factors. P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (Before)	-2.3132	0.2221	-10.42	**< 0.0001**
Collection (After)	0.6795	0.1536	4.42	**< 0.0001**

Table S2.11. Moths collected in flight intercept traps at control sites were counted, and data were pooled across collection dates and across traps within sites. I here present the coefficients from the best fitting GLMM with Poisson errors testing whether forest type predicted the number of moths collected. Sampling effort was included in the full model as a fixed predictor, and site was included as a random factor. Significant P-values ($\alpha \leq 0.05$) are indicated in bold.

Fixed effects	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept (From Native)	5.1907	0.1904	27.26	**<0.0001**
Forest type (From Plantation)	0.5690	0.0933	6.10	**<0.0001**

Appendix 3

A.3.1 DNA-barcoding detailed methods

I removed a leg from each wasp, crushed it, and performed a DNA extraction using the prepGEM™ Insect kit and method (www.zygem.com). To amplify the extracted DNA I used the following general insect primers for the Folmer region of the Cytochrome c Oxidase subunit I (COI) of the mitochondrial DNA:

HCO2198 (Folmer) - TAAACTTCAGGGTGACCAAAAAATCA
LCO1490 (Folmer) - GGTCAACAAATCATAAAGATATTGG

(Folmer *et al.*, 1994), and the KAPA Blood PCR Kit and method (www.kapabiosystems.com). I used gel electrophoresis to check that each extraction and amplification had produced DNA segments of the right length (approximately 658 base pairs). I cleaned the amplified DNA using the *GenCatch* PCR Purification Kit (www.epochlifescience.com), and sent the cleaned DNA to Macrogen Inc. (Seoul, Korea) for Sanger sequencing. I used the software *MEGA* version 5 (Tamura *et al.*, 2011) to align and trim the non-conserved parts of the sequences (i.e. the 'junk' DNA from the amplification process). I then calculated pair-wise similarity between each pair of sequences as outlined in the main text.

A.3.2 Supplementary tables and figures for Chapter 3

Table S3.1. To test whether my herbivore reduction treatment had the desired effect, I fitted a generalized linear mixed model with a Poisson distribution, and caterpillar abundance as the response variable. The predictors were collection (two levels: with the two before-herbivore-reduction collections pooled into one "before" sample vs. the two after-herbivore-reduction collections pooled into one "after" sample), treatment (herbivore reduction vs. control) and the collection-treatment interaction as fixed effects. Forest type, nested within site, nested within block were included as random factors to account for the non-independence of repeated measures at the before and after times. Here I present coefficients from the best model. Bold p-values indicate significance at $\alpha = 0.05$. The significant interaction between herbivore reduction treatment and collection ($p = 0.0015$), suggests that caterpillar abundance was initially greater at herbivore reduction sites, but after the herbivore reduction treatment, caterpillar abundance was significantly lower at treated sites than at control sites.

	Estimate	**Std. Error**	**z-value**	**P-value**
Intercept (Control, Before)	3.4023	0.2370	14.35	**<0.0001**
Treatment (Herbivore reduction)	0.7457	0.3248	2.30	**0.0217**
Collection (After)	0.0829	0.3258	0.25	0.7992
Treatment (Herb. reduc.)*Collection (After)	-1.4659	0.4611	-3.18	**0.0015**

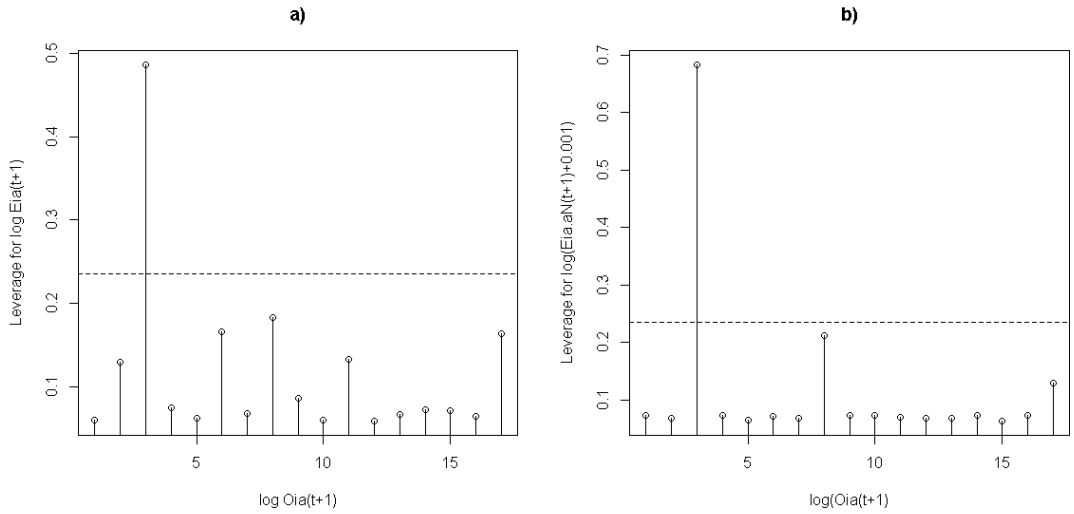

Figure S3.1. In my analyses of whether **a)** total expected parasitism rate could predict non-zero observed parasitism rate, and **b)** expected parasitism rate due to hosts in the native forest could predict non-zero observed parasitism rate, the third data point exerted much higher leverage, h_i, on the model fit than I might desire, where h_i is calculated as:

$$h_i = \frac{1}{n} + \frac{(x_i - \bar{x})^2}{\sum (x_j - \bar{x})^2}$$

where x is expected parasitism rate (log ($E_{ia(t+1)}$+0.001)), and n is the sample size. The dotted line is at $h_i = 2p/n$, where p is the number of parameters in the model, and above the dotted line a point may be considered highly influential (Crawley 2007).

Table S3.2. Coefficients from the best-fitting model in which parasitism, $O_{ia(t+1)}$ (as a binary response variable) was predicted by log (+0.001) expected parasitism rate ($E_{ia(t+1)}$), host habitat, and the interaction between expected parasitism rate and host habitat. The model was a generalized linear mixed effects model, with a binomial distribution, and block and site within block as random factors. P-values in bold indicate significance at $\alpha = 0.05$.

Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept (Plantation)	3.946	3.371	1.17	0.2417
$E_{ia(t+1)}$ (Plantation)	2.160	0.724	2.98	**0.0029**
$Habitat_A$ (Native)	13.839	6.390	2.17	**0.0303**
$E_{iA(t+1)}$:$Habitat_A$ (Native)	2.099	1.177	1.78	0.0744

Table S3.3. Coefficients from the best-fitting model testing whether **total** expected parasitism rate, (log($E_{ia(t+1)}$)), could predict non-zero observed parasitism rate, $O_{ia(t+1)}$, both **a)** without, and **b)** with an outlier that exerted unduly high leverage on the model (see Fig. S1a). The model was a generalized linear mixed effects model, with a binomial distribution, and block and site within block were included as random factors. $Habitat_A$ and the interaction between expected parasitism rate and $habitat_A$ were removed from the full model during model selection. P-values in bold are significant at $\alpha = 0.05$.

a) Without the outlier				
Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept	0.4191	0.6629	0.63	0.5273
Log($E_{ia(t+1)}$)	0.5577	0.1833	3.04	**0.0024**
b) With the outlier				
Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept	0.5147	0.6385	0.81	0.4202
Log($E_{ia(t+1)}$)	0.5884	0.1736	3.39	**0.0007**

Table S3.4. Coefficients from the best-fitting model testing whether expected parasitism rate due to shared parasitism with hosts in **native forest**, log ($E_{iajN(t+1)}$+0.001), could predict non-zero observed parasitism rate, $O_{ia(t+1)}$, both **a)** without, and **b)** with an outlier that exerted unduly high leverage on the model (see Fig. S1b). The model was a generalized linear mixed effects model, with a binomial distribution, and block and site within block were included as random factors. The interaction between $habitat_A$ and log($E_{iajN(t+1)}$+0.001) was removed from the full model during model selection. P-values in bold are significant at $\alpha = 0.05$.

a) Without the outlier				
Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept (Native)	2.2708	0.8990	2.53	**0.0115**
Log($E_{iAjN(t+1)}$+0.001) (Native)	0.6156	0.1658	3.71	**0.0002**
$Habitat_A$ (Plantation)	-1.6840	0.4731	-3.56	**0.0004**
b) With the outlier				
Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept (Native)	2.2883	0.8885	2.58	**0.0100**
Log($E_{iAjN(t+1)}$+0.001) (Native)	0.6188	0.1639	3.78	**0.0002**
$Habitat_A$ (Plantation)	-1.6899	0.4710	-3.59	**0.0003**

Table S3.5. Coefficients from the best-fitting model testing whether expected parasitism rate due to shared parasitism with hosts in **plantation forest**, log ($E_{iajP(t+1)}$+0.001), could predict non-zero observed parasitism rate, $O_{ia(t+1)}$. The model was a generalized linear mixed effects model, with a binomial distribution, and block and site within block were included as random factors. P-values in bold are significant at $\alpha = 0.05$.

Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept	-0.1861	0.4951	-0.38	0.7070
Log($E_{iajP(t+1)}$+0.001)	0.2920	0.1140	2.56	**0.0104**

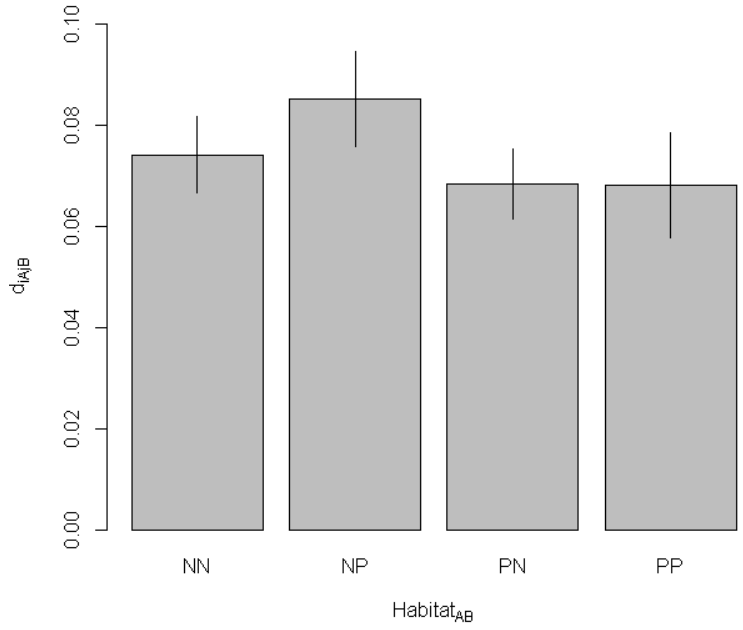

Figure S3.2. Magnitude of the apparent competitive effect on host species *i* in habitat *A* on host species *j* in habitat *B*. 'N' and 'P' refer to native forest and plantation forest, respectively, such that, for example, 'NP' refers the situation where host *i* is in native forest and host *j* is in plantation forest. Magnitude of d_{iAjB} was not significantly different across levels of $habitat_{AB}$ (p = 0.206).

A.3.3 Supplementary analysis for Chapter 3

In the main text, my analysis of whether expected parasitism rate significantly predicted observed parasitism rate excluded the contribution to expected parasitism rate made by within-habitat intraspecific effects (i.e. cases where $i = j$ AND $A = B$). This is because within-habitat intraspecific indirect effects have been previously demonstrated (e.g., Tack *et al.*, 2011), whereas cross-habitat intraspecific effects and interspecific effects at a community scale – whether cross- or within-habitat – have not been previously demonstrated. I wanted to focus on whether the latter two types of effect were detectable, as separate from any contribution of within-habitat indirect effects. However, I here present the equivalents of Figure S3.1 and Tables S3.3, S3.4, and S3.5, but with expected parasitism rate calculated from the full set of quantitative food web data, not excluding within-habitat intraspecific effects.

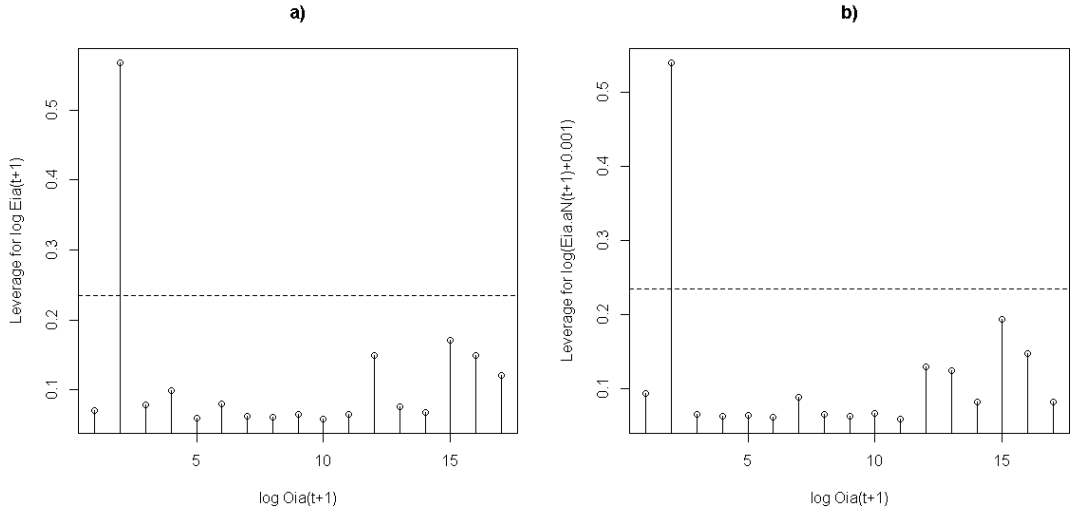

Figure S3.3. In my analyses of whether **a)** total expected parasitism rate could predict non-zero observed parasitism rate, and **b)** expected parasitism rate due to the native forest could predict non-zero observed parasitism rate, the second data point exerted much higher leverage, h_i, on the model fit than I might desire, where h_i is calculated as in Fig.S1.

Table S3.6. Coefficients from the best-fitting model testing whether **total** expected parasitism rate, log($E_{ia(t+1)}$), calculated from the full dataset, including all intra- and interspecific effects, could predict non-zero observed parasitism rate, $O_{ia(t+1)}$, both **a)** without, and **b)** with an outlier that exerted unduly high leverage on the model. The model was a generalized linear mixed effects model, with a binomial distribution, and block and site within block were included as random factors. $Habitat_A$ and the interaction between $habitat_A$ and expected parasitism rate were removed from the full model during model selection. P-values in bold are significant at $\alpha = 0.05$.

a) Without the outlier				
Fixed effects:	Estimate	Standard Error	z-value	P-value
Intercept	0.5913	0.6112	0.97	0.3333
Log($E_{ia(t+1)}$)	0.9274	0.2712	3.42	**0.0006**
b) With the outlier				
Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept	0.6146	0.6005	1.02	0.3061
Log($E_{ia(t+1)}$)	0.9389	0.2653	3.54	**0.0004**

Table S3.7. Coefficients from the best-fitting model testing whether expected parasitism rate due to shared parasitism with hosts in **native forest**, log($E_{iajN(t+1)}$+0.001), calculated from the full dataset, including all intra- and interspecific effects, could predict non-zero observed parasitism rate, $O_{ia(t+1)}$, both **a)** without, and **b)** with an outlier that exerted unduly high leverage on the model (see Fig. S3.3b). The model was a generalized linear mixed effects model, with a binomial distribution, and block and site within block were included as random factors. P-values in bold are significant at $\alpha = 0.05$.

a) Without the outlier				
Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept	0.6037	0.5679	1.06	0.2878
Log($E_{iajN(t+1)}$+0.001)	0.6672	0.1986	3.36	**0.0008**
b) With the outlier				
Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept	0.6407	0.5493	1.17	0.2434
Log($E_{iajN(t+1)}$+0.001)	0.6805	0.1918	3.55	**0.0004**

Table S3.8. Coefficients from the best-fitting model testing whether expected parasitism rate due to shared parasitism with hosts in **plantation forest**, log ($E_{iajP(t+1)}$+0.001), calculated from the full dataset, including all intra- and interspecific effects, could predict non-zero observed parasitism rate, $O_{ia(t+1)}$. The model was a generalized linear mixed effects model, with a binomial distribution, and block and site within block were included as random factors. P-values in bold are significant at $\alpha = 0.05$.

Fixed effects	Estimate	Standard Error	z-value	P-value
Intercept (Plantation)	2.1305	1.6071	1.33	0.1849
Log($E_{iajP(t+1)}$+0.001) (Plantation)	1.2912	0.5803	2.23	**0.0261**
$Habitat_A$ (Native)	-2.1389	1.6737	-1.29	0.2013
Log($E_{iAjP(t+1)}$+0.001)*$Habitat_A$ (Native)	-0.9463	0.6365	-1.49	0.1371

A.3.4 References

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3, 294-299.

Tack, A.J.M., Gripenberg, S., Roslin, T., 2011. Can we predict indirect interactions from quantitative food webs? - an experimental approach. Journal of Animal Ecology 80, 108-118.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA5: Molecular Evolutionary Genetics Analysis Using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. Molecular Biology and Evolution 28, 2731-2739.

Appendix 4

A.4.1 Supplementary tables for Chapter 4

Table S4.1. Coefficients from the best-fitting model testing whether (quantitative) traits of a host pair can predict their potential for apparent competition, (logit-transformed d_{ij}). The full model contained the fixed predictors abundance, body size, proportional generality of the host-parasitoid web (Prop.Gen.HP), proportional generality of the plant-herbivore web, quantitative closeness centrality (Q.centrality), (all log-transformed), and all interactions. Dataset and host pair identity were included as random factors. P_{MCMC}-values in bold are significant at $\alpha = 0.05$.

Fixed effects :	**Estimate**	**Standard Error**	**t-value**	**p_{MCMC}-value**
Intercept	-3.5105	0.6727	-5.22	**0.0332**
Abundance	0.1539	0.0281	5.48	**0.0001**
Prop.Gen.HP	0.1921	0.0740	2.60	**0.0130**
Q.centrality	0.4879	0.0815	5.99	**0.0001**
Abun.:Prop.Gen.HP	0.0220	0.0129	1.70	0.0792

Table S4.2. Coefficients from the best-fitting model testing whether (binary) traits of a host pair can predict their potential for apparent competition, logit d_{ij}. The full model contained the fixed predictors abundance, body size, normalized degree for the host-parasitoid web (N.Deg.HP), normalized degree for the plant-host web, binary closeness centrality, (all log-transformed), and all interactions. Dataset and host pair identity were included as random factors. P_{MCMC}-values in bold are significant at $\alpha = 0.05$.

Fixed effects :	**Estimate**	**Std. Error**	**t-value**	**p_{MCMC}-value**
Intercept	-3.5385	0.6170	-5.74	**0.0450**
Abundance	0.1260	0.0283	4.45	**0.0001**
Size	-0.1898	0.1122	-1.69	0.0834
Centrality	1.5173	0.4771	3.18	**0.0016**
N.Deg.HP	0.2926	0.0777	3.77	**0.0001**
Abun:Size	-0.1954	0.0556	-3.52	**0.0002**
Abun:Centrality	0.3097	0.1667	1.86	0.0638
Size:Centrality.	-6.9734	0.9524	-7.32	**0.0001**
Abun:N.Deg.HP	-0.0813	0.0254	-3.20	**0.0008**
Size:N.Deg.HP	1.3109	0.1807	7.26	**0.0001**
Centrality:N.Deg.HP	0.7678	0.2717	2.83	**0.0024**
Abun:Size:Centrality	0.0030	0.3620	0.01	0.9544
Abun:Size:N.Deg.HP	0.0037	0.0543	0.07	0.9758
Abun:Centr:N.Deg.HP	0.0502	0.0340	1.48	0.1224
Size:Centr:N.Deg.HP	0.2506	0.5942	0.42	0.6810
Abun:Size:Centr:N.Deg.HP	0.2297	0.0793	2.90	**0.0020**

A.4.2 Description of interactions in the model in which binary host traits predicted d_{ij} (Table S4.2)

There was a negative two-way interaction between host abundance ratio and host size ratio, in that the increase in the potential for apparent competition associated with an increase in host abundance ratio significantly decreased with an increase in size ratio. This suggests that hosts of greatly different sizes do not share parasitoids, so beyond a certain difference in size, there is no longer an effect of host abundance ratio on the potential for apparent competition. There were similar negative interactions between host size ratio and host centrality ratio, and between host size ratio and host normalized degree ratio. Again, these suggest that the increases in potential for apparent competition associated with increasing ratio of host centrality and with increasing ratio of number of parasitoids attacking each species of a pair of hosts, do not occur beyond a certain level of difference in body sizes of the host pair.

There was also a negative interaction between host abundance ratio and host normalized degree ratio, whereas each of these variates alone was a positive predictor of the potential for apparent competition. This suggests that when the host abundance ratio is high, the ratio of the number of parasitoid species attacking the hosts becomes less important in predicting the potential for apparent competition, and vice versa.

There was a positive interaction between host normalized degree ratio and host centrality ratio. This suggests that hosts that are attacked by a large number of parasitoid species, AND which are very central in the network, have a disproportionately larger potential for apparent competitive effects on less connected and less central hosts than if only one of these specifications was true.

Finally, there was a positive four-way interaction between host abundance ratio, size ratio, centrality ratio, and normalized degree ratio. That is, more abundant hosts have greater apparent competitive effects on less abundant hosts, the greater the difference in abundance, unless the hosts are of very different size, in which case the difference in abundance does not matter as greatly. However, if the hosts have very different connectedness and centrality as well as very different size, then abundance ratio is again a useful predictor.

Although all of the above interactions are significant in the binary model, the effect sizes are not large enough to cause obviously separate clusters within plots of d_{ij} versus abundance or normalized degree, or binary closeness centrality (Figs. 4.1a,d,e). As well, these interactions were significant only in models in which binary as opposed to quantitative metrics were used. Therefore caution should be used in interpreting these interactions (Banasek-Richter *et al.*, 2004).

A.4.3 References

Banasek-Richter, C., Cattin, M.F., Bersier, L.F., 2004. Sampling effects and the robustness of quantitative and qualitative food-web descriptors. Journal of Theoretical Biology 226, 23-32.